HERB ABUNDANCE AND DIVERSITY AMONG FIRE SEVERITY CLASSES IN PINE-OAK FORESTS OF GREAT SMOKY MOUNTAINS NATIONAL PARK

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ABSTRACT

HERB ABUNDANCE AND DIVERSITY AMONG FIRE SEVERITY CLASSES IN PINE-OAK FORESTS OF GREAT SMOKY MOUNTAINS NATIONAL PARK

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Fire suppression in forest ecosystems has changed fire regimes and modified woody plant composition, structure, and function throughout the US. Specific effects on the herbaceous plant communities are largely unknown. My study quantified herbaceous plant abundance and diversity of xeric pine-oak forests across four fire severity classes ("no burn", low, moderate, high) in four different fires occurring within the last seven years in Great Smoky Mountains National Park (GRSM). Fire severity was determined using Landsat data and strip transects were used to sample vegetation. Herb and subshrub cover combined was low and averaged only 5.86% (ranging 0.025 to 28.25%) across all fire severities. Herb cover and richness were significantly greater in high severity areas. These areas also had low litter-duff depth and high canopy openness. Litter-duff depth and subshrub cover, which were negatively related to herbs, explained variation in herb cover, richness, and diversity, while greater canopy openness was an important factor for increased herb cover. Specifically, eudicot forbs, ferns, and graminoids were associated with high severity areas. Historically, the herb species *Schizacyrium scoparium* and *Pteridium aquilinum* were historically dominant or co-dominant with subshrubs in xeric pine-oak forests, but this was only the case in high severity areas in this study. In contrast to these responses, subshrub abundance and non-graminoid monocot presence were not related to

fire severity. Reduced litter-duff depth, non-herb cover, and generally higher herb cover, richness, and diversity occurred in late growing season fire with a high Keetch-Byram Drought Index (KBDI) compared to early growing season fires with a low KBDI. These results indicate that higher severity fires maintain herbaceous communities in these ecosystems. However, high fire severity may not be favorable to several species of non-graminoid monocots. Finally, since subshrub and herb cover responded differently to fire severity, these plant groups should be considered separately in fire effects studies.

CHAPTER 1: INTRODUCTION

Xeric (dry) pine-oak forests in Great Smoky Mountains National Park (GRSM) are characterized by yellow pines such as *Pinus virginiana* Mill., *P. pungens* Lamb., *P. rigida* Mill., and *P. echinata* Mill. and oaks *Q. montana* Willd., *Q. coccinea* Münchh., *Q. velutina* Lam., and *Q. alba* L. (Whittaker 1956). Fires set by Native Americans for about the last 4,000 years likely maintained xeric pine-oak forests on ridges where people hunted and gathered food (Delcourt and Delcourt 1997; Fesenmyer and Christensen 2010). In this forest type, Harmon (1982) determined an average fire interval of 12.7 years between 1856 and 1940 in GRSM. After establishment of GRSM in 1934, shade-tolerant, fire-sensitive tree species such as *Acer rubrum* L. and *Nyssa sylvatica* Marshall increased in density in xeric pine-oak forests (Harrod et al. 1998) following fire suppression (Harmon 1982). In addition to changes in woody species composition, fire suppression reduced herbaceous species abundance and richness (Burton et al. 2011; Ducey et al. 1996; Harrod et al. 2000; Scharenbroch et al. 2012).

A goal of NPS is to conserve and restore ecosystems, including those that are fire-adapted (NPS 2009). In 1996, the National Park Service (NPS) stopped suppressing lightning-caused fires and used prescribed fire in dry areas of western GRSM as a management tool to conserve the fire-adapted ecosystems (Harrod and White 1999). Several studies have examined how fire affects woody species composition, structure, and function in the southern Appalachians (e.g., Abla 2014; Barden 1979; Harrod and White 1999; Knebel and Wentworth 2007; Thomas-Van Gundy et al. 2015). Fewer studies included the ground layer of non-woody and woody plants, typically defined as the herbaceous layer up to one meter in height (Elliott et al. 1999;

Elliott and Vose 2010; Elliott et al. 2009; Reilly et al. 2006). Thus, how fire affects herbaceous plant communities in forested ecosystems of the southern Appalachians is not well understood.

Goals of GRSM's Fire Effects Monitoring Program include using fire in xeric pine-oak forests to increase herbaceous abundance, richness, and diversity; decrease presence of shade-tolerant, fire-sensitive tree species like *A. rubrum*; and increase dominance of yellow pines (Rob Klein, GRSM Fire Ecologist, personal communication). Recent studies in GRSM are associated with determining how well using fire is meeting these goals (Harrod et al. 2000; Holzmueller et al. 2009; Jenkins et al. 2011). The goal of my thesis research is to improve our understanding of post-fire herbaceous plant communities in xeric pine-oak forests of GRSM. This knowledge can help predict how prescribed fire used in restoration efforts for the threatened xeric pine-oak forest type is also affecting the associated herbaceous communities. Furthermore, this study provides a better understanding of herbaceous changes following fires of different severities that can help the GRSM Fire Effects Monitoring Program improve their fire management planning. The results of my study not only apply to GRSM but should also be applicable to other southern Appalachian xeric pine-oak forests.

The following chapters of this thesis include a literature review, manuscript, literature-cited, and appendices. The literature review (Chapter 2) summarizes sub-mesic, sub-xeric, and xeric plant communities of the southern Appalachians; factors affecting herbaceous species composition, diversity, and abundance; and fire effects on forest communities. The manuscript (Chapter 3) is intended for submission to Forest Ecology and Management. The literature-cited chapter (Chapter 4) contains citations corresponding to all in-text citations in the thesis. Appendix A includes additional data analyses tables and figures, and Appendix B contains and a

short description of methods and results of a spring pilot study conducted prior to the summer research described in the manuscript chapter.

CHAPTER 2: LITERATURE REVIEW

Forest Communities of Great Smoky Mountains National Park

Sub-Mesic and Sub-Xeric Forests

Mesophication, the improving environmental conditions for shade-tolerant, fire-sensitive plant species that has led to the decline of fire-tolerant, shade-intolerant species (Nowacki and Abrams 2008), caused by fire suppression has increased the abundance of sub-mesic and sub-xeric species occurring on xeric sites (Barden and Woods 1976; Flatley et al. 2015; Harmon 1984; Harrod et al. 1998; Thomas-Van Gundy et al. 2015). Sub-mesic tree species include *Acer rubrum* L., *Carya glabra* (Mill.) Sweet, *Carya alba* (L.) Nutt. ex Elliott, *Quercus rubra* L., and *Cornus florida* L., with *Q. rubra* dominant above 1220 m in elevation (Whittaker 1956). *Carya* (hickory) species have decreased in dominance, while *Quercus* (oaks) spp., *A. rubrum*, and *Liriodendron tulipifera* L. are more dominant (Jenkins 2007; Madden et al. 2004). *Rhododendron maximum* L., *Gaylussacia ursina* (M.A. Curtis) Torr. & A. Gray ex A. Gray, *Pyrularia pubera* Michx., and *Calycanthus floridus* L. are frequently found in the shrub layer below 1070 m, and *Vaccinium corybosum* L. and *Rhododendron calendulaceum* (Michx.) Torr. are more common above this elevation (Whittaker 1956). Herbs in sub-mesic forests include *Aureolaria laevigata* (Raf.) Raf., *Polystichum acrostichoides* (Michx.) Schott, *Medeola virginiana* L., and *Maianthemum racemosum* (L.) Link (Whittaker 1956). Sub-mesic forests correspond most closely to what Jenkins et al. (2007) calls montane oak-hickory forests, which occupy 31% of GRSM and can occur on any aspect.

Sub-xeric sites historically were dominated by *Quercus montana* Willd. and *Castanea dentata* (Marshall) Borkh. below 1220 m, with *Q. montana* replaced by *Q. alba* L. and *Q. rubra*

at higher elevations (Whittaker 1956). Since the decline of *C. dentata* (Woods and Shanks 1959), Jenkins et al. (2007) notes that *Q. montana, Q. coccinea* Münchh., *Pinus strobus* L., and *Q. alba* have dominated the chestnut oak forest type. *R. maximum, Kalmia latifolia* L., and *G. ursina* occupy the shrub layer (Jenkins 2007; Whittaker 1956). *Galax urceolata* (Poir.) Brummitt is dominant among herb and subshrub species (Jenkins 2007; Whittaker 1956), with the herbs *Campanula divaricata* Michx. and *A. laevigata* and subshrub *Chimaphila maculata* (L.) Pursh present (Whittaker 1956). Sub-xeric forests constitute 15% of GRSM (Madden et al. 2004). When a large disturbance occurs on mesic, sub-mesic, or sub-xeric sites, early successional forests can be dominated by *Robinia pseudoacacia* L., *A. rubrum*, and *L. tulipifera* (Jenkins 2007; Madden et al. 2004; McGrath and Clatterbuck 2013; Phillips and Shure 1990), with *P. strobus* and *Betula lenta* L. also present (Jenkins 2007; Madden et al. 2004). Early successional forests comprise about 6% of GRSM (Madden et al. 2004).

Xeric Forests

Xeric pine-oak forests typically occur in the western part of GRSM on dry, exposed ridges and slopes that face south, southwest, or west (Callaway et al. 1987; Golden 1981; Jenkins 2007; Whittaker 1956). This forest type constitutes about 9% of GRSM (Madden et al. 2004). The forest has about 30% canopy openness, which allows light to penetrate to the understory (Whittaker 1956). Xeric ridge forests have nutrient-poor and acidic soils (Jenkins 2007), and the soil is often no more than 15 cm deep (Cain 1931). Yellow pines (*Pinus virginiana* Mill., *P. pungens* Lamb., *P. rigida* Mill., and *P. echinata* Mill.) and oaks (*Q. montana, Q. coccinea, Q. velutina* Lam., and *Q. alba*) characterize the canopy (Whittaker 1956). *P. virginiana* dominates at the low elevations (below 670 m), *P. rigida* dominates at the middle elevations 670 – 975 m, and *P. pungens* dominates at the high elevations (above 975 m) (Whittaker 1956). Although

regeneration of *P. pungens* relies on fire to release seed from its serotinous cones, it has been able to survive during fire suppression because about 40% of its cones release seeds after two years, regardless of the presence of fire (Barden 1979). The other cones remain closed and the seeds can be viable for up to ten years (Barden 1979).

Oxydendrum arboreum (L.) DC. and *Acer rubrum* historically occupied the sub-canopy of xeric pine-oak forests, and *Nyssa sylvatica* was sparse in the canopy (Cain 1931; Whittaker 1956). Fire suppression has increased the dominance of *A. rubrum* and other more mesic plant species (Flatley et al. 2015; Harmon 1984; Harrod et al. 1998; Thomas-Van Gundy et al. 2015); reduced yellow pine regeneration (Brose and Waldrop 2006; Flatley et al. 2015; Harrod and White 1999); and increased canopy density, basal area, and canopy species richness overall (Harrod et al. 1998). The historic average fire interval, determined by fire dendrochronology and fire scars, was 12.7 years in western GRSM (Harmon 1982) but has been extended to 60 or more years with fire suppression. It could take many years to return xeric pine-oak forests to pre-fire suppression canopy species composition and forest structure (Harmon 1984). Because of fire suppression, *Dendroctonus frontalis* Zimmermann (southern pine beetle) infestation is another threat to xeric pine-oak forests (Schowalter et al. 1981), where it has decreased yellow pine basal area and density (Knebel and Wentworth 2007). Reestablishing fire in uninfested xeric pine-oak forests has been reported to reduce yellow pine mortality caused by the southern pine beetle (Knebel and Wentworth 2007).

In the understory of xeric pine-oak forests, there is generally a high abundance of heath shrubs, with *Kalmia latifolia* or *Vaccinium pallidum* Aiton dominant, and *V. hirsutum* Buckley, *V. stamineum* L., *Gaylussacia baccata* (Wangenh.) K. Koch (Cain 1931; Whittaker 1956), and *G. ursina* (M.A. Curtis) Torr. & A. Gray ex A. Gray (Cain 1931) occurring; however, shrub

cover can vary between 10 and 90% (Whittaker 1956). Herb cover in xeric pine-oak forests is low (less than 20%); by contrast, herb cover in cove forests can be as high as 80% (Whittaker 1956). Herb cover is as low as 2-10% in low-elevation *Pinus virginiana* forests, generally 5-20% in mid-elevation *P. rigida* heaths and high-elevation *P. pungens* heaths, and there is a positive relationship between herb cover and elevation on these sites (Whittaker 1956). Eudicot forbs found in the xeric pine-oak forest type include *Solidago* spp., *Coreopsis major* Walter (Harrod et al. 2000; Whittaker 1956), *Eurybia surculosa* (Michx.) G.L. Nesom, and *Lespedeza* spp. (Harrod et al. 2000). Non-graminoid monocots (such as lilies, orchids, and irises) that occur include *Cleistes bifaria* (Fernald) Catling & Gregg, *Platanthera ciliaris* (L.) Lindl., and *Aletris farinosa* L. (Cain 1931). A common fern in this forest type is *Pteridium aquilinum* (L.) Kuhn (Cain 1931; Harrod et al. 2000; Whittaker 1956). Graminoids include *Schizachyrium scoparium* (Michx.) Nash and *Dichanthelium* spp. (Harrod et al. 2000; Whittaker 1956) as well as *Sorghastrum nutans* (L.) Nash (Harrod et al. 2000). Descriptions of the forest structure and species before decades of fire suppression took place (Cain 1931; Whittaker 1956) can be used as reference conditions to restore herbs in xeric pine-oak forests. GRSM was logged prior to the park's establishment, which created early successional habitat across the park. Recent studies in xeric pine-oak forests suggest that fire can increase herbaceous cover to between 20 and 30%, while unburned areas had 1 to 6% cover (Harrod et al. 2000; Jenkins et al. 2011). However, Harrod et al. (2000) showed that herb cover peaked at 21-24% in years 3, 4, and 8 after fire, with a decline to 4% cover by year 12 likely due to decreased light availability. Herb richness has also been shown to increase after fire on these sites (Harrod et al. 2000; Jenkins et al. 2011).

Factors Affecting Herbaceous Abundance, Composition, and Diversity

Two primary factors that affect plant abundance and species composition are stress and disturbance (Callaway et al. 1987; Elliott et al. 2002; Elliott et al. 2012; Golden 1981; Grime 1977; Keddy and Maclellan 1990). Elevation, topography (aspect and how exposed or sheltered an area is), soil moisture, and soil type (including pH and water-holding capacity) are environmental variables corresponding to the stress factor (Callaway et al. 1987; Golden 1981; Petersen and Drewa 2009; Whittaker 1956). The percentage of subsoil clay (Golden 1981; Mowbray and Oosting 1968) and the clay-to-sand ratio, which is related to soil aeration and soil moisture availability (Mowbray and Oosting 1968), are also important in determining plant species composition and abundance. For example, the sub-mesic-to-xeric oak and pine forests have among the highest percent subsoil clay in GRSM (Golden 1981). These forests also experience the hottest temperatures, are well-drained, and tend not to be at high elevations (Golden 1981). Tree diversity also varies with elevation and is highest between cove forests and chestnut oak forests at about 900 m (Whittaker 1956), which is at mid-elevation for GRSM. Tree species are also associated with microclimates of differing soil pH (Finzi et al. 1998) that can affect understory plant composition and abundance. For example, nutrients are less available to plants in more acidic soils (Jensen 2010) on exposed slopes and ridges (Jenkins 2007) where xeric pine-oak forests occur. Other edaphic characteristics that affect herbaceous plant composition and diversity are depth and organic matter. C_3 grasses were more strongly positively related to soil organic matter than C_4 grasses in oak barrens of southern Ohio (Petersen and Drewa 2009). Shallow soil depth means plants do not have access to water sources deeper in the soil when the surface-level soil dries, which favors stress-tolerant herb species. Sheltered, low-elevation slopes with moist soil, where mesic cove forests occur (Golden 1981), have high

herbaceous abundance and species richness (Small and McCarthy 2002) and understory diversity (Huebner et al. 1995) compared to exposed, drier slopes. Northwest- and southeast-facing slopes typically have high soil fertility that also corresponds to high herb abundance and richness (Small and McCarthy 2002).

Disturbance is the other important factor that, together with stress, determines patterns of plant species composition and abundance (Grime 1977) found throughout GRSM (Harmon et al. 1984). According to Grime (1977), a competitive plant strategy seems more likely to be exhibited by species in cove forests where there is sheltered topography and high moisture (Cain 1931), and disturbance does not maintain these forests. On xeric sites such as dry, exposed south-facing slopes (Golden 1981) stress-tolerant species establish, but with frequent fire the ruderal strategy is also favored. With fire suppression and a shift to more mesic forests, competitive species are more likely to occur.

In general, low to moderate disturbances in the southern Appalachians include small harvest openings, understory fires, wind, and drought (Elliott et al. 2011). A dense tree canopy can limit the amount of sunlight reaching the ground layer, which restricts herbaceous diversity to shade-tolerant species (Vazquez-Yanes et al. 1990). Increasing canopy openness generally leads to increased herb cover and diversity (Cipollini et al. 2012; Elliott et al. 2012; Harrod et al. 2000; Huisinga et al. 2005; Jenkins et al. 2011; Sabo et al. 2009; Small and McCarthy 2002). Wind disturbance has shown to create a more heterogeneous forest structure compared to a clear-cut (McGrath and Clatterbuck 2013). Ground layer abundance, species richness, and Shannon diversity also increased after wind disturbance (Elliott et al. 2002). However, oak regeneration does not appear to be promoted by wind disturbance because oak seedling density (White et al. 2014) and survivorship (Berg 2004) are lower when compared to undisturbed areas. Drought,

measured by the Keetch-Byram Drought Index (KBDI), causes increased fuel consumption during a fire (Jenkins et al. 2011; Reid et al. 2012), increased herbaceous cover and species richness after the fire (Jenkins et al. 2011), and increased pine regeneration (Barden and Woods 1976; Jenkins et al. 2011). Extreme drought can also directly result in *Q. velutina* mortality but *Q. montana* and yellow pines are more drought-resistant (Hursh and Haasis 1931).

Xeric pine-oak forest species compete effectively on dry, high solar irradiation ridges (Callaway et al. 1987; Golden 1981; Whittaker 1956), but without fire these forests experience species shifts due to mesophication (Barden and Woods 1976; Flatley et al. 2015; Harmon 1984; Harrod et al. 1998; Thomas-Van Gundy et al. 2015). The amount of resprouting after moderate severity disturbance decreases from sub-mesic to xeric sites because xeric sites contain more yellow pine individuals, which reestablish through seedlings (Harmon et al. 1984). High severity disturbance is needed for yellow pines to become dominant in the canopy because shading due to rapidly resprouting species after lower severity disturbance prevents pine seedlings from surviving (Welch et al. 2000).

Severely disturbed areas have higher temperature, relative humidity, soil compaction, and lower litter (undecomposed organic matter) depth compared to mature forests (Small and McCarthy 2002). Severe (Griffis et al. 2001; Huisinga et al. 2005; Sabo et al. 2009) or frequent (Burton et al. 2011) disturbance can also lead to an increase in native and non-native herbaceous colonizers. Invasive species generally reduce plant diversity (Hanula et al. 2009; Hejda et al. 2009). However, native species such as the southern pine beetle in xeric pine-oak forests can also become detrimental when ecosystem function changes due to factors such as fire suppression (Knebel and Wentworth 2007; Schowalter et al. 1981). *Odocoileus virginianus* Zimm. (white-tailed deer) herbivory can cause reductions in herbaceous cover and diversity

(Griggs et al. 2006; Thiemann et al. 2009), and some herbaceous species only occur when deer are excluded (Griggs et al. 2006). Woody plant diversity is also affected by herbivore preference. For example, *Tsuga canadensis* (L.) Carrière and *Liquidambar styraciflua* L. are less preferred and dominate where herbivory is heavy (Griggs et al. 2006).

Diseases caused by several fungal and bacterial pathogens such as powdery mildews, rusts, leaf spots, blights, and rots can negatively affect herbaceous plants (Beckerman and Lerner 2009), and how widespread the disease is mostly dictates its effect on the ecosystem. The decline of *Castanea dentata* with the introduction of the chestnut blight (*Cryphonectria parasitica* [Murrill] Barr) in 1904 resulted in a fundamental change in species composition in eastern forests, and led to the replacement of what was once a dominant species mostly with *Quercus montana*, *Q. rubra*, and *Acer rubrum* in GRSM (Woods and Shanks 1959). On xeric sites, *C. dentata* was mostly replaced by *Oxydendrum arboreum*, *Q. coccinea*, and *Pinus rigida* (Woods and Shanks 1959).

Fire Effects on Forest Communities

Fire (or burn) severity is a measure of the extent of environmental change in a burned area due to the fire. This can be estimated in the field by providing a quantitative Composite Burn Index (CBI) rating (Wimberly and Reilly 2007), which incorporates canopy and understory mortality as well as duff (decomposing organic matter below the litter layer) depth reduction. The US Geological Survey (USGS) and NPS created the National Burn Severity Mapping Project so that fire severity classes on national park lands can be assessed using Landsat imagery. Fire severity is determined using Landsat by first calculating the Normalized Burn Ratio (NBR) using the following equation: $NBR = 1000 \times (R_4 - R_7)/(R_4 + R_7)$ (Verbyla et al. 2008; Wimberly and Reilly 2007). R_4 and R_7 are light reflectance values for Landsat bands 4 and 7, respectively.

Band 4 reflects green vegetation, while band 7 reflects soil and rocks (Rocchio 2013). After fire, there is a decrease in the amount of near-infrared reflectance (0.76-0.96 μm wavelengths) detected by band 4 and an increase in shortwave infrared reflectance (2.08-2.34 μm wavelengths) detected by band 7 (Verbyla et al. 2008). Fire severity classes are quantitatively described using the differenced Normalized Burn Ratio (dNBR) and calculated using the following equation: $dNBR = NBR_{pre\text{-}fire} - NBR_{post\text{-}fire}$ (Verbyla et al. 2008; Wimberly and Reilly 2007). Higher dNBR values signify higher fire severity.

Fire (Hagan et al. 2015) and particularly high severity fire (Arthur et al. 1998; Barden and Woods 1976; Groeschl et al. 1993; Jenkins et al. 2011; Vose et al. 1997; Welch et al. 2000), typically results in high yellow pine regeneration compared to unburned areas in the southern Appalachians. High severity fire that opens the canopy (Brown et al. 2014; Cocke et al. 2005; Groeschl et al. 1992; Huisinga et al. 2005; Scharenbroch et al. 2012; Welch et al. 2000), reduces duff depth (Cocke et al. 2005; Groeschl 1991; Huisinga et al. 2005; as reviewed in Knoepp et al. 2005), reduces total fuel load (Brown et al. 2014), and kills buds of hardwood species (Welch et al. 2000) will lead to yellow pine regeneration. Growing season fires produce similar effects as high severity fires, with increased pine dominance, increased oak mortality (Glitzenstein et al. 1995), reduced resprouting (Drewa et al. 2002), reduced leaf litter depths (Gruchy et al. 2009; Harrod et al. 2000), and reduced shrub cover (Harrod et al. 2000) compared to dormant season fires. Late growing season fires during a severe drought result in increased yellow pine regeneration (Barden and Woods 1976; Jenkins et al. 2011), increased fuel consumption (Jenkins et al. 2011; Reid et al. 2012), thinner duff depth, decreased overstory and understory woody density, and decreased total fuel load compared to early growing season fires (Jenkins et al. 2011). In contrast to high severity fires, low severity (Arthur et al. 1998; Welch et al. 2000) and

dormant season (Petersen and Drewa 2009; 2014) fires lead to rapid hardwood species resprouting and further dominance of hardwoods over yellow pines due to the shade created (Welch et al. 2000).

There are mixed results concerning the effects of fire on understory species. Many studies have shown an increase in understory species richness and diversity after fire (Ducey et al. 1996; Elliott et al. 1999; Elliott et al. 2009; Elliott et al. 2012; Groeschl et al. 1992; Hagan et al. 2015; Holzmueller et al. 2009; Reilly et al. 2006; Welch et al. 2000) and particularly after high severity fire (Brown et al. 2014; Huisinga et al. 2005). Some studies noted increased understory abundance after fire in oak forests of New England (Ducey et al. 1996), xeric pine-oak forests of the southern Appalachians (Elliott et al. 2012), and ponderosa pine forests of northern Arizona (Huisinga et al. 2005). In contrast to increased responses, other studies found no difference in understory abundance and diversity (Burton et al. 2011; Ducey et al. 1996; Holzmueller et al. 2009) or only minor increases in understory abundance and richness (Hutchinson et al. 2005) after fire. Others noted decreased understory cover after fire, particularly of *Kalmia latifolia* (Hagan et al. 2015; Jenkins et al. 2011; Schwartz et al. 2016; Vose et al. 1997; Welch et al. 2000). These differing results may be related to the species being studied, the forest type, and time since the fire (Burton et al. 2011; Elliott et al. 2012; Petersen and Drewa 2014).

Herb cover, species richness, and species diversity generally increase after one (Elliott et al. 2012; Harrod et al. 2000; Huisinga et al. 2005; Jenkins et al. 2011; Pourreza et al. 2014; Scharenbroch et al. 2012; Schwartz et al. 2016) and multiple fires (Burton et al. 2011; Hagan et al. 2015; Schwartz et al. 2016) across different forest types. However, the relationship with multiple fires is not always consistent (Holzmueller et al. 2009). There are also mixed results

about the effects of fire season on herbaceous species. Gruchy et al. (2009) reported increased legume cover after growing season compared to dormant season fire, while Sparks et al. (1998) found higher cover of certain legume and graminoid species after dormant season fire. Because of this, varying the seasonality of fire may generally have the greatest overall positive effect on herbaceous diversity (Hiers et al. 2000). However, late growing season fires appear to be best for increasing herb cover and richness in xeric pine-oak forests of the southern Appalachians (Jenkins et al. 2011), which is likely due to the environmental conditions typically created by these and high severity fires. Herbaceous cover has been shown to be positively related to canopy opening (Harrod et al. 2000; Jenkins et al. 2011; Sabo et al. 2009; Small and McCarthy 2002) and negatively related to litter and duff depth (Jenkins et al. 2011; Sydes and Grime 1981; Vazquez-Yanes et al. 1990), understory woody density, and total fuel load (Jenkins et al. 2011; Schwartz et al. 2016), but no correlation between herb cover and litter depth has also been found (Harrod et al. 2000).

High severity fire has been shown to increase herbaceous cover (Harrod et al. 2000; Jenkins et al. 2011) and species richness (Huisinga et al. 2005), but Pourreza et al. (2014) reported higher herbaceous species cover, richness, and diversity in low and moderate severity compared to high severity areas one year after a fire, while Wang and Kemball (2005) reported no difference in herb cover among fire severities four years after fire. The results of Pourreza et al. (2014) can be explained by the findings of Harrod et al. (2000) who noted that herb cover in xeric pine-oak forests of GRSM was lowest and dominated by *P. aquilinum* one year after fire (3% herb cover), increased and was dominated by *Erechtites hieraciifolius* (L.) Raf. ex DC. two and three years after fire, and from year 8, when dominated by *Schizachyrium scoparium*, to year 12 after fire decreased to approximately first-year cover. Low herb cover one year after high

severity fire appears to be due to soil heating (Gagnon et al. 2015), with high severity areas exhibiting a diminished viable seed bank compared to unburned areas (Maia et al. 2012). The seed bank may be mostly unchanged (Keyser et al. 2012) or increase in viable seed density after low severity fire (Maia et al. 2012), potentially due to the presence of smoke (Crosti et al. 2006; Jefferson et al. 2008). Soil microbial biomass, respiration, and invertebrate diversity were also unaffected by low severity fire (Scharenbroch et al. 2012), but high severity fire areas had decreased soil microbial biomass (Prieto-Fernandez et al. 1998), which slows nutrient cycling. Fire severity is positively related to soil nutrient availability (Groeschl 1991; as reviewed in Knoepp et al. 2005; Scharenbroch et al. 2012), but increased nutrient availability typically lasts only a few years because plants quickly take up the nutrients (as reviewed in Knoepp et al. 2005).

CHAPTER 3: MANUSCRIPT:
HERB ABUNDANCE AND DIVERSITY AMONG FIRE SEVERITY CLASSES IN PINE-OAK FORESTS OF GREAT SMOKY MOUNTAINS NATIONAL PARK

Introduction

Xeric pine-oak forests typically occur on dry, exposed ridges and slopes that face south, southwest, or west in the southern Appalachians (Callaway et al. 1987; Golden 1981; Jenkins 2007; Whittaker 1956). Yellow pines (*Pinus virginiana* Mill., *P. pungens* Lamb., *P. rigida* Mill., and *P. echinata* Mill.) and oaks (*Quercus montana* Willd., *Q. coccinea* Münchh., *Q. velutina* Lam., and *Q. alba* L.) dominate the canopy (Whittaker 1956). These forests are believed to be maintained by relatively frequent fire (Brose and Waldrop 2006). For example, the average fire interval in Great Smoky Mountains National Park (GRSM) was 12.7 years between 1856 and 1940 (Harmon 1982) when human-caused fires and logging were prevalent. Yellow pine regeneration in the southern Appalachians occurred consistently from the late 1700s to the early 1900s (Brose and Waldrop 2006) but stopped around the mid-1900s (Brose and Waldrop 2006; Harrod and White 1999) when fire suppression policies were implemented in the region (Harmon 1982). Fire suppression resulted in increased dominance of more mesic plant species such as *Acer rubrum* L. (Harmon 1984; Harrod et al. 1998; Thomas-Van Gundy et al. 2015), reduced yellow pine (Brose and Waldrop 2006; Flatley et al. 2015; Harrod and White 1999) and oak (Harrod and White 1999) regeneration, and increased *Dendroctonus frontalis* Zimmermann (southern pine beetle) infestations in xeric pine-oak forests (Knebel and Wentworth 2007; Schowalter et al. 1981). These infestations resulted in decreased yellow pine density and basal area (Knebel and Wentworth 2007), but fire suppression led to increased canopy density, basal

area, and canopy species richness overall in xeric pine-oak forests (Harrod et al. 1998). This creates cooler, moister conditions below the canopy that perpetuate more mesic species.

Fire (or burn) severity is a measure of the extent of environmental change in a burned area due to the fire. Fire severity classes ("no burn", low, moderate, and high) can be determined using pre- and post-fire Landsat imagery. Canopy openness increases (Brown et al. 2014; Cocke et al. 2005; Groeschl et al. 1992; Huisinga et al. 2005; Scharenbroch et al. 2012; Welch et al. 2000) and litter and duff (compacted, decomposing leaves, twigs, and other organic matter) depth decreases (Cocke et al. 2005; Groeschl 1991; Huisinga et al. 2005; as reviewed in Knoepp et al. 2005; Schwartz et al. 2016) after fire, particularly in higher severity areas. Without fire, a thick duff layer can prevent seeds from germinating (Vazquez-Yanes et al. 1990), and a dense canopy limits light availability to herbs. Understory woody cover, especially of *Kalmia latifolia*, has been shown to decrease after fire (Hagan et al. 2015; Schwartz et al. 2016; Vose et al. 1997; Welch et al. 2000), which reduces competition for light and space, thereby increasing yellow pine (Vose et al. 1997) and herb establishment.

Herbaceous cover, species richness, and species diversity generally increase after one fire (Elliott et al. 2012; Harrod et al. 2000; Huisinga et al. 2005; Jenkins et al. 2011; Pourreza et al. 2014; Scharenbroch et al. 2012) or more than one fire (Burton et al. 2011; Hagan et al. 2015). High severity fire in particular has resulted in increased herb cover (Harrod et al. 2000; Jenkins et al. 2011) and species richness (Huisinga et al. 2005). Conversely, Pourreza et al. (2014) reported higher herbaceous species cover, richness, and diversity in low and moderate severity compared to high severity areas one year after a fire in Zagros oak forests of Iran. These results can be explained by the findings of Harrod et al. (2000) who noted that herb cover in xeric pine-oak forests of GRSM was lowest one year after fire (3% herb cover), increased two and three

years after fire, and from year 8 to year 12 after fire decreased to approximately first-year cover. Low herb cover one year after high severity fire appears to be due to soil heating (Gagnon et al. 2015), with high severity areas exhibiting a diminished viable seed bank compared to unburned areas (Maia et al. 2012). The seed bank may be mostly unchanged (Keyser et al. 2012) or increase in viable seed density after low severity fire (Maia et al. 2012), potentially due to the presence of smoke (Crosti et al. 2006; Jefferson et al. 2008). Herb cover was shown to be negatively related to litter or duff depth (Jenkins et al. 2011; Sydes and Grime 1981; Vazquez-Yanes et al. 1990), understory density, and total fuel load (Jenkins et al. 2011; Schwartz et al. 2016), and positively related to canopy openness (Harrod et al. 2000; Jenkins et al. 2011; Sabo et al. 2009; Small and McCarthy 2002), which are conditions created by high fire severity, late growing season fire, and a high Keetch-Byram Drought Index (KBDI) during a fire (Jenkins et al. 2011).

Fire seasonality affects responses to fire, which is likely due to different fire severities that occur during the year. Growing season fire can increase oak mortality and pine dominance (Glitzenstein et al. 1995) while reducing hardwood resprouting (Drewa et al. 2002). These fires, like high severity fires, reduce leaf litter depths (Gruchy et al. 2009; Harrod et al. 2000) and shrub cover (Harrod et al. 2000) compared to dormant season fire. However, responses related to season of fire can vary with herbaceous species (Gruchy et al. 2009; Sparks et al. 1998). Varying the seasonality of fire may generally have the greatest positive effect on herbaceous diversity (Hiers et al. 2000), but late growing season fire appears to be best for increasing herb cover in xeric pine-oak forests of the southern Appalachians (Jenkins et al. 2011).

Recent studies in xeric pine-oak forests of GRSM suggest that regularly occurring fire (2-8 year interval) can maintain herbaceous cover at 20-30%, while fire-suppressed areas typically

had 1-6% cover (Harrod et al. 2000; Jenkins et al. 2011). Herb richness has also been shown to increase after fire in xeric pine-oak forests (Harrod et al. 2000; Jenkins et al. 2011). Eudicot forbs found in the xeric pine-oak forest type include *Solidago* spp., *Coreopsis major* Walter (Harrod et al. 2000; Whittaker 1956), *Eurybia surculosa* (Michx.) G.L. Nesom, and *Lespedeza* spp. (Harrod et al. 2000). Non-graminoid monocots (such as lilies, orchids, and irises) that occur include *Cleistes bifaria* (Fernald) Catling & Gregg, *Platanthera ciliaris* (L.) Lindl., and *Aletris farinosa* L. (Cain 1931). A common fern in this forest type is *Pteridium aquilinum* (L.) Kuhn (Cain 1931; Harrod et al. 2000; Whittaker 1956). Graminoids include *Schizachyrium scoparium* (Michx.) Nash and *Dichanthelium* spp. (Harrod et al. 2000; Whittaker 1956) as well as *Sorghastrum nutans* (L.) Nash (Harrod et al. 2000).

Although much research has been conducted in the southern Appalachians on how fire directly and indirectly affects woody species composition, structure, and function (e.g., Abla 2014; Barden 1979; Harrod and White 1999; Knebel and Wentworth 2007; Thomas-Van Gundy et al. 2015), much less is known about on how herbaceous plant communities respond to fire. Of the studies that have been done, many did not distinguish the responses to fire by non-woody species from woody vines, shrubs, and trees in the ground layer (Elliott et al. 1999; Elliott and Vose 2010; Elliott et al. 2009; Reilly et al. 2006). Studies that did focus on herbaceous communities also included subshrubs, such as *Galax urceolata*, in the herbaceous species category (Harrod et al. 2000; Holzmueller et al. 2009). The purpose of my research was to improve our knowledge of how herbaceous communities in xeric pine-oak forests respond to different fire severity classes. My specific research questions are:

1. Is there a difference in herbaceous species abundance, richness, diversity, and species composition among fire severity classes ("no burn", low, moderate, and high)?

2. Is there a positive or negative relationship between herbaceous species abundance, richness, and diversity and canopy openness, litter-duff depth, non-herb cover, and subshrub cover?

Methods

Study Sites

I chose four previously burned areas (fires) on the western side of GRSM in Tennessee, USA (Figure 1). All four areas burned once since the establishment of GRSM in 1934 according to the park's fire history maps, and each of these fires occurred within the last seven years prior to when the fieldwork was conducted: the oldest burned in 2008 and the youngest burned in 2014 (Table 1). Calderwood occurred late in the growing season during a drought, while the other three fires occurred early in the growing season (Table 1). According to the GRSM disturbance history map, the early growing season fires were not heavily cut prior to the creation of the park and have been part of GRSM since its establishment. Calderwood was acquired about 15 years ago (Rob Klein, GRSM Fire Ecologist, personal communication) and has been intensively treated for invasive plant species (Kristine Johnson, GRSM Supervisory Forester, personal communication). Yellow pine, yellow pine-oak, or oak-yellow pine forest types were selected from a GRSM GIS layer of dominant vegetation (Madden et al. 2004) to represent xeric pine-oak forests within the burned areas and outside them for the "no burn" areas. These forest types included a combination of yellow pine (*Pinus virginiana*, *P. rigida*, *P. pungens*, and *P. echinata*) and oak species (*Quercus velutina, Q. coccinea, Q. montana,* and *Q. alba*). Landsat-based fire severity maps provided by the GRSM Fire Effects Monitoring Program (Gatlinburg, TN), such as illustrated in Figure 2, were used to identify areas of different fire severity classes within fires. It has been documented that Landsat identifies fire severity

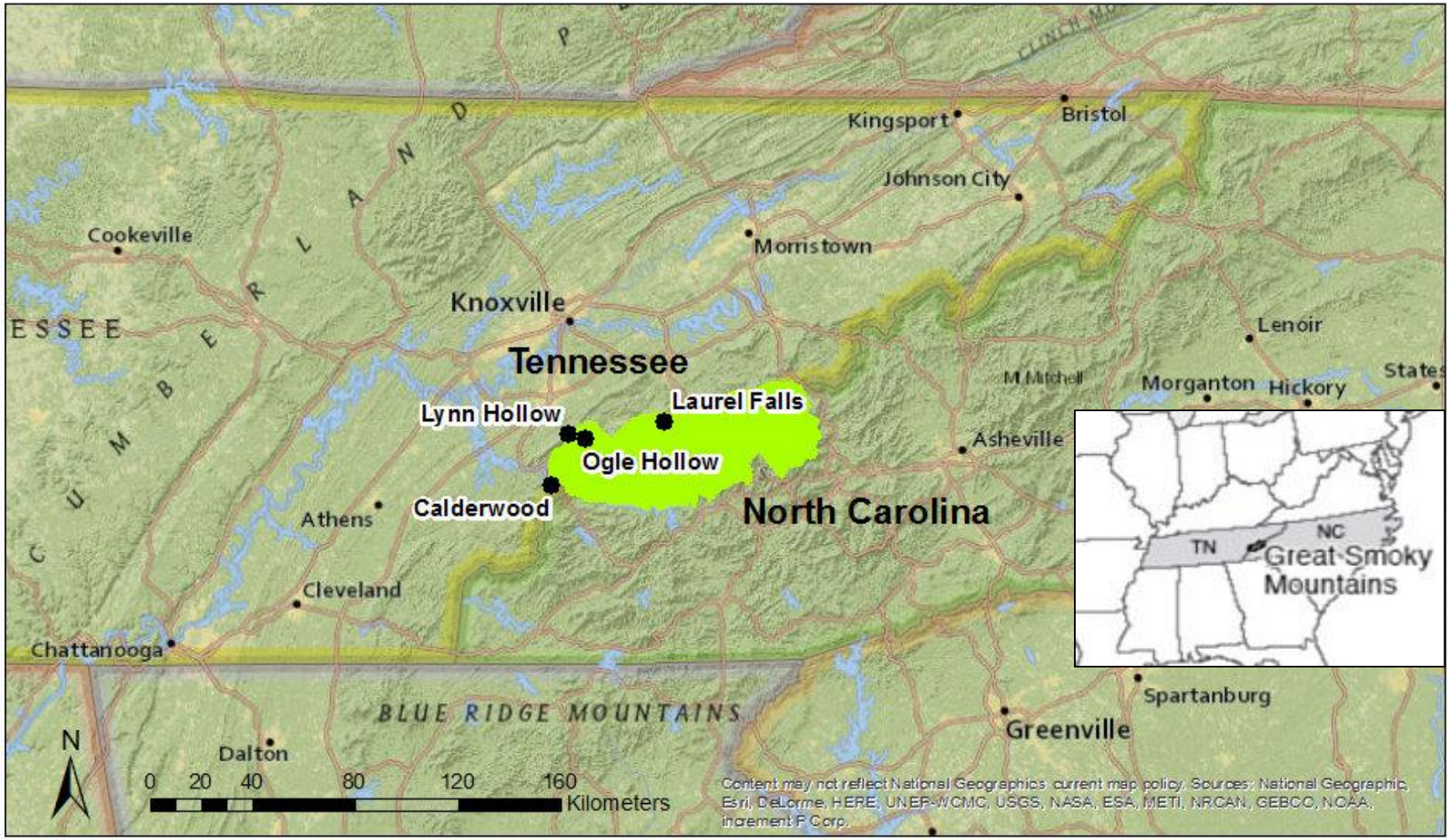


Figure 1: Locations of the four fires sampled in Great Smoky Mountains National Park, Tennessee, USA. Inset map adapted from Penn State College of Earth and Mineral Sciences: Textbook 4.1: Still more plate tectonics, the Great Smoky Mountains. Available from: https://www.e-education.psu.edu/geosc10/l4_p2.html

Table 1: Fires studied in GRSM. Slope, elevation, aspect, and Landsat band 4 pre-fire reflectance values of transects are recorded as mean ± SE. The Keetch-Byram Drought Index (KBDI) ranges from 0 to 800, and higher values signify more extensive drought.

Fire Name	Fire Start - End	Size (ha)	Ignition Source	KBDI	Duff Depth Reduction[1]	Slope (%)	Elevation (m)	Aspect (°)	Pre-fire Landsat Band 4
Calderwood	Aug. 17 - Sept. 9, 2010	73	Lightning	715	50-75%	41 ± 2	510 ± 18	239 ± 7	114 ± 2
Ogle Hollow	Apr. 24 - 26, 2008	139	Escaped Prescribed Fire	78	< 25%	38 ± 3	585 ± 7	213 ± 13	98 ± 2
Lynn Hollow	Apr. 1, 2014	100	Prescribed	21	< 25%	45 ± 4	560 ± 9	189 ± 9	80 ± 1
Laurel Falls	Apr. 27 - May 3, 2009	104	Escaped Campfire	83	< 25%	48 ± 2	854 ± 18	185 ± 7	137 ± 4

[1]The percentage of duff depth reduced after the fire, which was determined by the GRSM Fire Effects Monitoring Program.

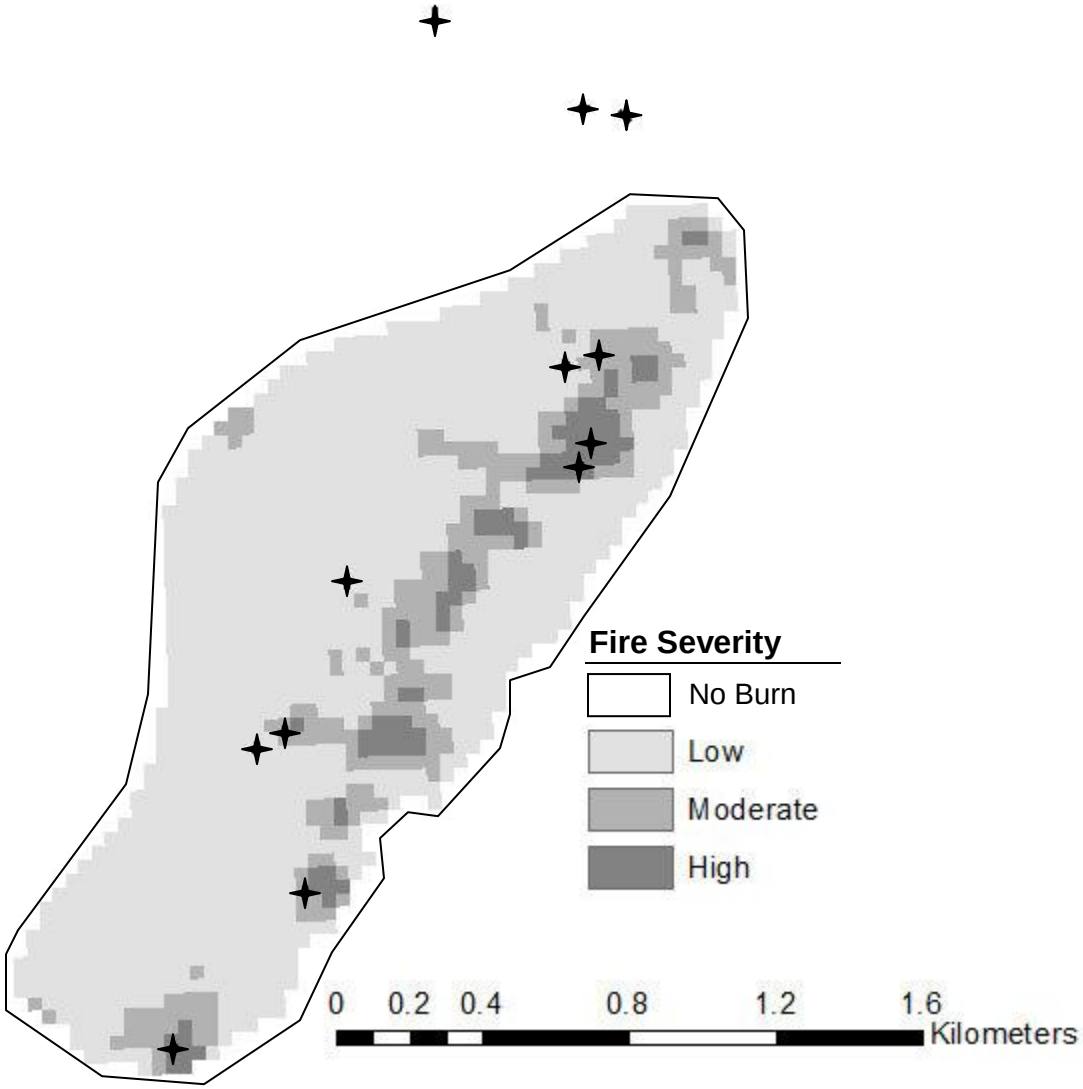


Figure 2: Fire severity map of Ogle Hollow with transects indicated by plus symbols, including those located outside of the fire.

consistently with the ground-based Composite Burn Index (CBI) (Abla 2014; Cocke et al. 2005). Fire severity was determined by dNBR as described by Wimberly and Reilly (2007), with a dNBR range of -150 to 80 representing low severity, 81 to 270 corresponding to moderate severity, and 271 and above signifying high severity areas within a fire (GRSM Fire Effects Monitoring Program). Areas less than 600 meters away from the fire perimeters that had not burned since GRSM's inception, according to the park's fire history maps, were sampled as "no burn" areas.

Since pre-fire vegetation data were not available, variation in aspect, slope, elevation, soil type, and pre-fire vegetation conditions (based on Landsat band 4 reflectance values) were minimized across severity classes within fires. According to GRSM's soil taxonomic classification map, soil properties were the same within each fire for areas sampled in the Calderwood, Ogle Hollow, and Lynn Hollow fires. Calderwood had loamy, siliceous, mesic Lithic Dystrochrepts soil, and Ogle Hollow and Lynn Hollow had coarse-loamy, mixed, semiactive, mesic Typic Dystrudepts soil, which are well-drained soils. At Laurel Falls, six areas sampled had fine-loamy, mixed, subactive, mesic Typic Hapludults soil, which is also well-drained, and five transects had the same soil properties as sampled areas at Ogle Hollow and Lynn Hollow. One transect was located on a rock outcrop-Unicoi soil complex, which is excessively drained. Slope and aspect were measured in the field while elevation and Landsat band 4 values were determined on GIS after sampling. Statistical analysis was conducted to determine whether there was significant variation in these factors within fires. Slope, aspect, and elevation generally did not vary among areas sampled within a fire. At Ogle Hollow, aspect varied but all sampled areas were south- (moderate severity= 173°, high severity = 180°) or southwest-facing (low severity = 252°, no burn = 249°). No burn areas in the Calderwood fire

were significantly lower in elevation compared to the other severity classes (406 versus 536 – 551 m). At Lynn Hollow, slope of sampled areas varied but not consistently across severity classes, where high severity and no burn areas had steeper slopes (55-56%) than low severity areas (28%). Moderate severity areas averaged 41% slope. Pre-fire Landsat band 4 reflectance values, which reflect green vegetation (Rocchio 2013), did not differ significantly at any of the fires, indicating similar canopy and sub-canopy conditions. Areas to be sampled were relocated if the conditions in the field clearly did not represent the appropriate fire severity class based on overstory and understory mortality, or a pine-oak forest type.

Data Collection

Data collection occurred from June 28 to August 2, 2015. Areas were sampled using strip transects as described by Burnham and Anderson (1984). Strip transects were 20 m long and 2 m wide (Figure 3). Three strip transects were sampled in each of the four fire severity classes (no burn, low, moderate, and high) in each of the four fires (Calderwood, Ogle Hollow, Lynn Hollow, and Laurel Falls), with a total of 48 transects sampled. Strip transects allowed efficient sampling in xeric pine-oak forests where herbaceous species abundance was expected to be low (Harrod et al. 2000). A width of 2 m for the strip transect was chosen to avoid overlooking herbs, accurately estimate percent cover, and efficiently determine plant inclusion in the strip transect. Each transect was treated as an independent sample, with transects at least 13 m apart. Slope and aspect were measured at both ends of each transect in the field and the values were averaged. GIS was used to obtain the elevation and Landsat Band 4 data was used for the pre-fire condition values for both ends of each transect, and these were averaged. The data were used to verify uniformity of the sampled areas for environmental factors that could cause differences in vegetation not related to fire severity.

(a)

(b)

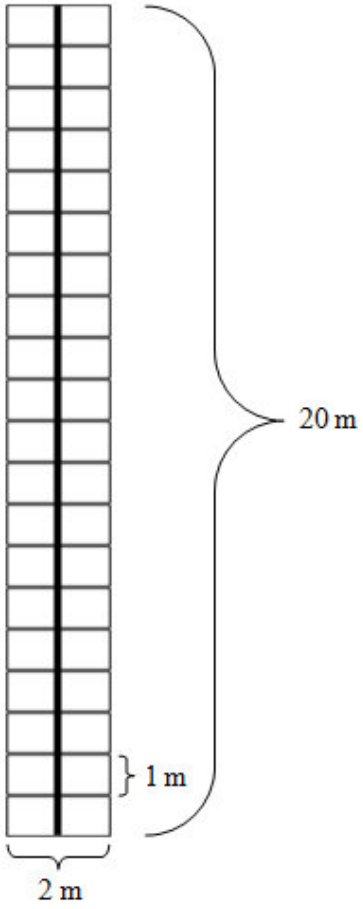


Figure 3: (a) One end of a strip transect with horizontal PVC pipes indicating part of the edges of the quadrat and 1 m out from each side of the vertical transect line in the center. (b) Diagram of a strip transect showing twenty 2 × 1 m quadrats.

Transects were divided into twenty 2 × 1 m quadrats. In each quadrat, herbaceous plants and subshrubs were identified, and a visual estimation of herb and subshrub percent cover of each species was recorded using the percent cover classes 0, 0-1, 1-5, 5-25, 25-50, 50-75, and 75-100% based on Pourreza et al. (2014). Herbs included forbs, graminoids, and fern allies. *Schizachyrium scoparium* (Michx.) Nash and *Andropogon virginicus* L. species could not be distinguished, so their abundance was recorded in one group. Subshrubs were defined as small woody plants that have a similar growth habit to herbs. In each quadrat, non-herb (including trees, shrubs, woody vines, moss, and large wood chunks and rocks) total cover was visually estimated and the top two dominant non-herbs were identified and their cover was recorded using the previously described cover class system (Pourreza et al. 2014). Non-herb cover included material up to 2.3 m above the ground. These data were collected to determine whether non-herb cover by shading or lack of space was related to herb species abundance, richness, and diversity. Non-herb cover did not include subshrubs. Subshrub data were collected separately because herbs and subshrubs occupy the same layer of the forest. Litter-duff depth was defined as the distance between the bottom of the decomposing organic layer to the top of the leaf litter layer, and was measured at the center of each quadrat. This was measured because a thick duff layer can prevent seeds from germinating (Vazquez-Yanes et al. 1990) and thus could reduce herbaceous species cover and diversity. Canopy openness was measured at four equally-spaced intervals along the transect at the 2.5, 7.5, 12.5, and 17.5 m marks. Canopy photographs were taken with an Opteka HDII 0.20X fisheye lens 2.3 m above the ground. The photographs were analyzed using Gap Light Analyzer 2.0 (Frazer et al. 1999) to quantify canopy openness and thereby the relative amount of light available to the understory.

Data Analyses

The R Foundation's R version 3.1.2 statistical software was used for Shannon diversity calculations, analyses of variance (ANOVAs), linear regression, multiple regression, and logistic regression. Slope, aspect, elevation, and Landsat band 4 reflectance values were compared across severities for each fire using one-way ANOVA to determine whether there were differences among fire severity classes for each variable. Fire was considered replication and, therefore, conditions were not matched to minimize variation among them. Diversity of herbs in each fire severity class was quantified using Shannon's Diversity Index. Variation in herb abundance, species richness, species diversity, subshrub cover, non-herb cover, litter-duff depth, and canopy openness was compared among fire severity classes using two-way ANOVAs with a 4×4 factorial design (four fires, four severity classes). Where variables differed significantly ($\alpha = 0.05$) among severity classes, Tukey tests were used to compare severities. Although fire was considered replication, variation among fires, such as fire seasonality, was examined because different conditions could help interpret plant responses to fire severity. No burn areas were not included in comparisons among fires. Levene homogeneity of variance tests were conducted on ANOVAs, and none of these were significant. Litter-duff depth, non-herb cover, canopy openness, and subshrub cover were used as covariates in ANCOVA to determine whether they also explained the variation in herb abundance, richness, and diversity observed among fire severity classes. These covariates were also examined using simple linear and multiple regression to determine whether they had a significant relationship with herb species abundance, richness, and diversity and subshrub cover. When relationships appeared to be nonlinear, log transformation of the data was conducted and the data were reanalyzed.

Because herb abundance was low, species were grouped to help examine species trends

within the herb community. Species were grouped by functional groups (eudicot forbs, ferns, graminoids, and non-graminoid monocots) and the length of their life cycle (perennial and annual-biennial). These groups were analyzed to determine whether ruderal-strategy species were more prevalent in certain severities compared to others. When analyzing by life cycle, only individuals that could be identified to species (rather than to genus or family) were included, unless all species in the genera have the same life cycle. Probability of herb species group occurrence was determined by logistic regression analysis of presence instead of percent cover; however, the number of transects in this study was low for this analysis.

PC-ORD 5.0 software (McCune and Mefford 2006) was used to conduct MRPP (multiple-response permutation procedures, Sorensen's [Bray-Curtis] distance measure) analysis and indicator species analysis (ISA) of herb species and species groups using a randomization test with 4999 permutations. This was done to determine whether herbaceous species composition differed among severity classes (MRPP) and to determine whether species or species groups were indicators of a particular fire severity (ISA). Bonferroni Corrections were used on uncorrected pairwise comparisons among fire severities produced by MRPP when analyzing herbs by functional groups and by life cycles. ISA provided observed indicator values, and the Monte Carlo test was used to determine their statistical significance. This software was also used to calculate first- and second-order jackknife estimators of species richness and to produce a species-area curve and distance curve using Sorensen's (Bray-Curtis) distance measure to evaluate dissimilarity of species composition among strip transects. The species-area curve and jackknife estimators were used to determine whether most of the herb species in xeric pine-oak forests were sampled during the study. Jackknife estimators were unbiased estimators of the true number of species of herbs, where the first-order jackknife estimate incorporates

species appearing in only one transect, and the second-order jackknife estimate incorporates species appearing in one or two transects and has a larger mean square error (Burnham and Overton 1979).

Results

Litter-duff depth ranged from 2.9 to 18.5 cm, averaged 8.7 cm, and tended to decrease with increasing fire severity. However, only no burn areas had significantly deeper depth than moderate and high severity areas ($p = 0.014$) (Table 2). Canopy openness ranged from 10.42 to 97.19%, averaged 35.37%, and was greater in moderate and high severity areas ($p < 0.001$) (Table 2). Non-herb cover (woody species excluding subshrubs, dead wood, moss, and large rocks) ranged from 21.37 to 85.00% and averaged 58.61%. It was lower in no burn and low severity areas ($p < 0.001$) (Table 2).

A total of 67 herbaceous species were identified across the 48 strip transects (Table 3). Of the species found, 27 occurred only in one transect and 14 were found in only two. The number of new species found in each transect decreased and the dissimilarity in herb species composition among transects approached zero as more transects were sampled (Figure 4). The first-order jackknife estimate of herb richness incorporating species found in one transect was 93.4 species, and the second-order jackknife estimate incorporating species found in one or two transects was 106.2 species. MRPP analysis that included all herb species indicated herbaceous species composition did not vary among fire severity classes ($p = 0.067$, $A = 0.015$) (Table 4). Herb cover across all transects ranged from 0 to 28.20% and averaged 2.86%. It was highest in high severity areas ($p < 0.001$) (Table 2). Herb and subshrub cover combined ranged from 0.025 to 28.25%, averaged 5.86%, and was also highest in high severity areas ($p = 0.004$). When including canopy openness as a covariate, herb cover as well as herb plus subshrub cover no

Table 2: Variation in herbs, subshrubs, non-herb cover, litter-duff depth, and canopy openness among fire severities (mean ± SE) in GRSM. Different letters indicate significant Tukey test pairwise comparison differences across fire severity class means. Herb diversity represents the Shannon Diversity Index.

		Fire Severity				
Variable	Overall Mean	No Burn	Low	Moderate	High	p-value
Herb Cover (%)	2.86	0.41 ± 0.16 a	0.76 ± 0.36 a	1.47 ± 0.95 a	8.78 ± 3.03 b	<0.001
Herb + Subshrub Cover (%)	5.86	2.79 ± 0.99 a	4.27 ± 1.49 a	4.92 ± 1.71 a	11.44 ± 2.91 b	0.004
Herb Richness (#)	5.3	2.6 ± 0.5 a	4.7 ± 1.4 ab	5.9 ± 2.1 ab	8.0 ± 1.2 b	0.003
Herb Diversity	0.89	0.62 ± 0.15	0.96 ± 0.24	0.86 ± 0.28	1.11 ± 0.15	0.197
Subshrub Cover (%)	3.00	2.38 ± 0.95	3.51 ± 1.59	3.45 ± 1.62	2.66 ± 1.34	0.866
Non-herb Cover (%)	58.61	51.03 ± 5.20 a	51.20 ± 5.34 a	65.91 ± 4.68 b	66.31 ± 4.55 b	<0.001
Litter-Duff Depth (cm)	8.7	10.5 ± 0.8 a	8.8 ± 0.7 ab	7.9 ± 0.6 b	7.7 ± 0.9 b	0.014
Canopy Openness (%)	35.37	19.81 ± 2.18 a	20.39 ± 1.70 a	33.43 ± 2.26 b	67.84 ± 4.77 c	<0.001

Table 3: Herbaceous and subshrub species percent cover recorded in four fires in GRSM (mean ± SE). All SE are <0.01% unless otherwise noted. Count indicates the number of strip transects in which a species occurred. See Table A1 for the family and authority of each species.

	Overall	----------Fire Severity----------				
	Mean	No Burn	Low	Moderate	High	Count
Eudicot Forbs						
Ageratina altissima	0.067	0	0.01±0.01	0.23±0.23	0.03±0.03	7
Amphicarpaea bracteata	0.002	0	0	0.01±0.01	0	1
Antennaria sp.	0.001	0	<0.01	0	0	1
Aristolochia serpentaria	0.001	0	0	<0.01	0	1
Coreopsis major	0.005	<0.01	0.01	0.01±0.01	0	5
Desmodium nudiflorum	0.002	0	<0.01	<0.01	0	3
Erechtites hieraciifolius	0.005	0	<0.01	<0.01	0.02±0.02	5
Eupatorium rotundifolium	0.003	0	<0.01	0	0.01±0.01	2
E. serotinum	0.002	0	0	<0.01	<0.01	2
E. sessilifolium	0.001	0	0	<0.01	0	1
Eurybia surculosa	0.019	0	0.01	0.01	0.06±0.05	9
Eutrochium purpureum	0.001	0	0	0	<0.01	1
Hieracium venosum	0.001	0	<0.01	0	0	1
Houstonia longifolia	0.001	0	0	<0.01	0	1
Lactuca sp.	0.001	0	0	<0.01	<0.01	2
Lespedeza hirta	0.035	0	0	0.01±0.01	0.13±0.13	2
L. repens	0.028	0	0	0.01±0.01	0.10±0.10	2
L. violacea	0.007	0	<0.01	0.02±0.02	0.01	5
Lespedeza sp.	0.008	0	0	<0.01	0.03±0.03	3
Lysimachia quadrifolia	0.304	0	0.26±0.26	0.13±0.09	0.83±0.48	8
Pycnanthemum sp.	0.005	0	0	0.02±0.02	0	1
Pityopsis graminifolia	0.091	0	0	0	0.36±0.36	1
Polygala polygama	0.002	0	0	<0.01	0.01±0.01	3
Potentilla sp.	0.002	0	0.01±0.01	<0.01	0	2
Pseudognaphalium obtusifolium	0.001	0	0	0	<0.01	1
Silphium asteriscus	0.029	0	0	0.11±0.11	0	1
Solidago arguta	0.043	<0.01	0.04±0.04	0.06±0.06	0.07±0.07	7
S. canadensis	0.004	0	0	0	0.01±0.01	1
S. curtisii	0.020	0	0.04±0.04	0.04±0.04	0	3
S. odora	0.023	<0.01	0	0	0.09±0.07	4
Solidago sp.	0.243	0.01±0.01	0.11±0.11	0.22±0.22	0.63±0.61	14
Stellaria sp.	0.001	0	0	0	<0.01	1
Symphyotrichum patens	0.002	0	0	0	0.01±0.01	2
S. undulatum	0.006	<0.01	<0.01	<0.01	0.02±0.02	6
Taenidia integerrima	0.002	0	0.01±0.01	0	0	1
Viola hastata	0.008	<0.01	0.02±0.01	0.01±0.01	0	6
V. palmata	0.002	0	<0.01	0.01±0.01	0	2
Viola sp.	0.001	0	<0.01	0	0	1
Asteraceae sp.	0.056	0	0	0	0.23±0.23	3

Table 3 Continued

Species	Overall Mean	Fire Severity: No Burn	Low	Moderate	High	Count
Ferns						
Asplenium montanum	0.001	0	0	0	<0.01	1
A. platyneuron	0.001	0	0	0	<0.01	1
Dennstaedtia punctilobula	0.014	0	0	0	0.05±0.05	2
Polystichum acrostichoides	0.002	0	0	0	0.01	2
Pteridium aquilinum	0.542	0.17±0.07	0.04±0.03	0.13±0.11	1.83±0.96	17
Graminoids						
Carex hirsutella	0.001	0	<0.01	0	0	1
Carex sp.	0.001	0	0	<0.01	0	1
Dichanthelium boscii	0.005	0	0	0.02±0.02	0	2
D. commutatum	0.081	0.02±0.01	0.05±0.03	0.07±0.05	0.17±0.13	26
D. dichotomum	0.007	0	0.02±0.02	0.01	0	6
D. villosissimum	0.002	0	0	0.01±.01	0	1
Dichanthelium sp.	0.001	0	0	0	<0.01	1
Microstegium vimineum	0.003	0	0	0.01±0.01	0	1
Schizachyrium scoparium/ Andropogon virginicus	1.044	0.03±0.01	0.03±0.03	0.24±0.22	3.89±2.81	20
Scleria sp.	0.034	0	0	0.03±0.02	0.10±0.05	13
Sorghastrum nutans	0.005	0	0	0	0.02±0.02	1
Cyperaceae sp.	0.002	0	<0.01	<0.01	0	2
Non-Graminoid Monocots						
Chamaelirium luteum	0.009	0.04±0.04	0	0	0	1
Cleistes bifaria	0.008	<0.01	0	0.01±0.01	0.02±0.02	5
Goodyera pubescens	0.001	0	<0.01	0	0	1
Hypoxis hirsuta	0.001	0	<0.01	0	0	1
Iris verna	0.026	0.10±0.10	0.01±0.01	0	0	4
Lilium michauxii	0.006	0.01±0.01	<0.01	0	0.01	5
Maianthemum racemosum	0.012	0.02±0.02	0.03±0.02	0	0	6
Platanthera ciliaris	0.002	0	0	<0.01	<0.01	2
Polygonatum biflorum	0.005	<0.01	0.02±0.02	0	0	2
Uvularia puberula	0.015	<0.01	0.02±0.01	0.01±0.01	0.03±0.03	7
Fern Ally						
Dendrolycopodium obscurum	0.001	0	<0.01	0	0	1
Subshrubs						
Chamaecrista nictitans	0.001	0	0	0	<0.01	1
Chimaphila maculata	0.042	0.07±0.07	0.06±0.04	0.03±0.02	0	17
Epigaea repens	0.128	0.27±0.21	0.14±0.09	0.07±0.06	0.04±0.04	13
Galax urceolata	1.511	0.61±0.21	2.63±2.40	2.05±1.29	0.75±0.62	22
Galium circaezans	0.003	0	0	0.01±0.01	0	1
Gaultheria procumbens	1.280	1.43±1.28	0.67±0.60	1.27±0.77	1.75±1.11	14
Hypericum hypericoides	0.004	0	0	0.01±0.01	<0.01	2
Mitchella repens	0.001	0	<0.01	0	0	1
Tephrosia virginiana	0.029	0	0	0	0.12±0.11	2

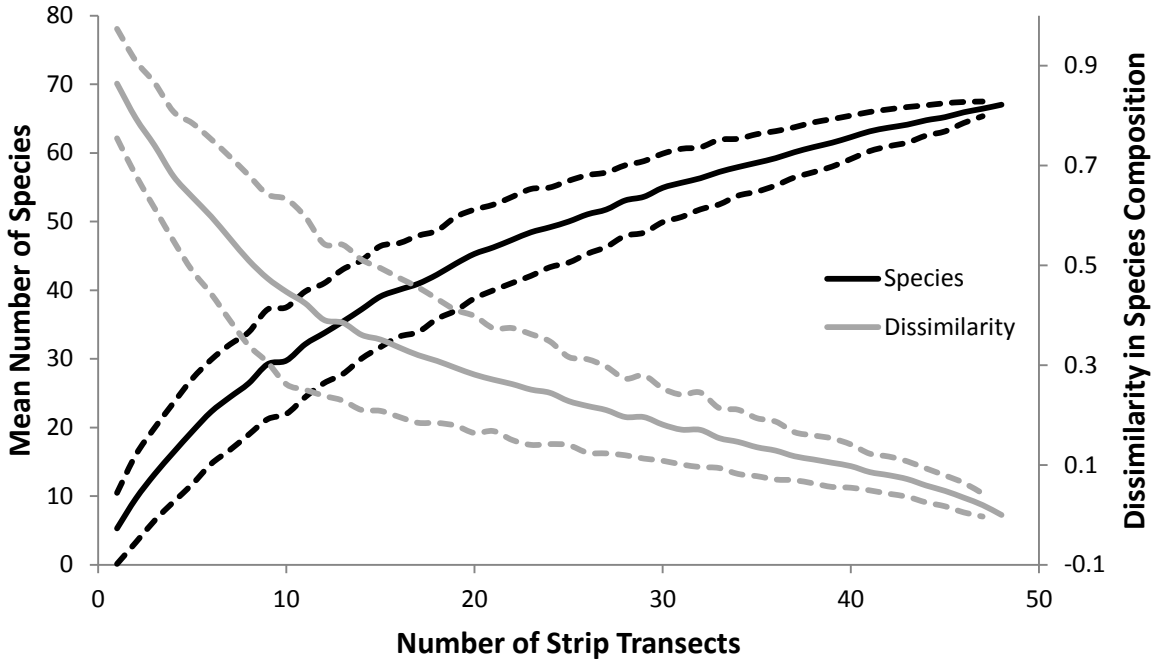


Figure 4: Species-area curve for strip transects. Dissimilarity in species composition is measured by Sorensen's (Bray-Curtis) distance. Solid lines are mean values and dotted lines are ± SD.

Table 4: Herb species composition variation among fire severity classes at GRSM. Pairwise comparisons are shown when the p-value was significant. After Bonferroni Corrections of pairwise comparisons ($\alpha = 0.0083$), p-values with an asterisk are significant. The A value estimates the proportion of Sorensen (Bray-Curtis) distances explained by species group and is similar to R^2 in a linear relationship.

Species Group[1]	MRPP p-value	A	Pairwise Comparisons among Severities	p-value
All Herbs	0.067	0.015	---	---
Functional Groups	0.030	0.030		
			No Burn vs. Low	0.578
			No Burn vs. Moderate	0.102
			No Burn vs. High	0.008*
			Low vs. Moderate	0.318
			Low vs. High	0.131
			Moderate vs. High	0.135
Life Cycle Groups	0.026	0.054		
			No Burn vs. Low	0.866
			No Burn vs. Moderate	0.181
			No Burn vs. High	0.008*
			Low vs. Moderate	0.349
			Low vs. High	0.056
			Moderate vs. High	0.065

[1]Functional groups include eudicot forbs, ferns, graminoids, and non-graminoid monocots. Life cycle groups include perennial and annual plus biennial herbs.

longer varied among fire severities ($p = 0.622$ and 0.446, respectively). No other covariates explained variation in herb cover or herb plus subshrub cover across fire severities. The relationship between herb cover and canopy openness was positive ($p < 0.001$, $R^2 = 0.366$), and with litter-duff depth it was negative ($p < 0.001$, $R^2 = 0.412$) (Table 5). No significant relationship was observed for herb cover and non-herb cover and between herb and subshrub cover. Of the 59.6% of variation in herb cover explained by all factors combined ($p < 0.001$), litter-duff depth explained the most variation followed by canopy openness and subshrub cover (Table 6).

Herbaceous species richness ranged from 0 to 23, averaged 5.3 species, and varied among fire severities ($p = 0.002$), but was only significantly greater in high severity areas compared to no burn areas (Table 2). However, there was a trend of increasing richness from no burn to high severity areas. No covariates explained variation in herb richness across fire severities, and herb richness and canopy openness were not significantly related. Richness varied negatively with litter-duff depth ($p < 0.001$, $R^2 = 0.392$), subshrub cover ($p = 0.002$, $R^2 = 0.185$), and non-herb cover ($p = 0.038$, $R^2 = 0.090$) (Table 5). Of the 55.9% of variation in herb richness explained by all factors combined ($p < 0.001$), litter-duff depth explained the most variation followed by subshrub cover (Table 6). Shannon Diversity Index of herbs ranged from 0 to 2.45, averaged 0.89, and did not vary among fire severity classes ($p = 0.197$) (Table 2). However, it decreased with increasing litter-duff depth ($p = 0.001$, $R^2 = 0.211$), subshrub cover ($p = 0.005$, $R^2 = 0.161$), and non-herb cover ($p = 0.006$, $R^2 = 0.151$) (Table 5). No significant relationship was observed between herb diversity and canopy openness. Of the 37.3% of variation in herb diversity explained by all factors combined ($p < 0.001$), litter-duff depth and subshrub cover explained the most and about the same amount of variation (Table 6).

Table 5: Linear relationships between herbs and litter-duff depth, non-herb cover, canopy openness, and subshrub cover. Herb diversity represents the Shannon Diversity Index.

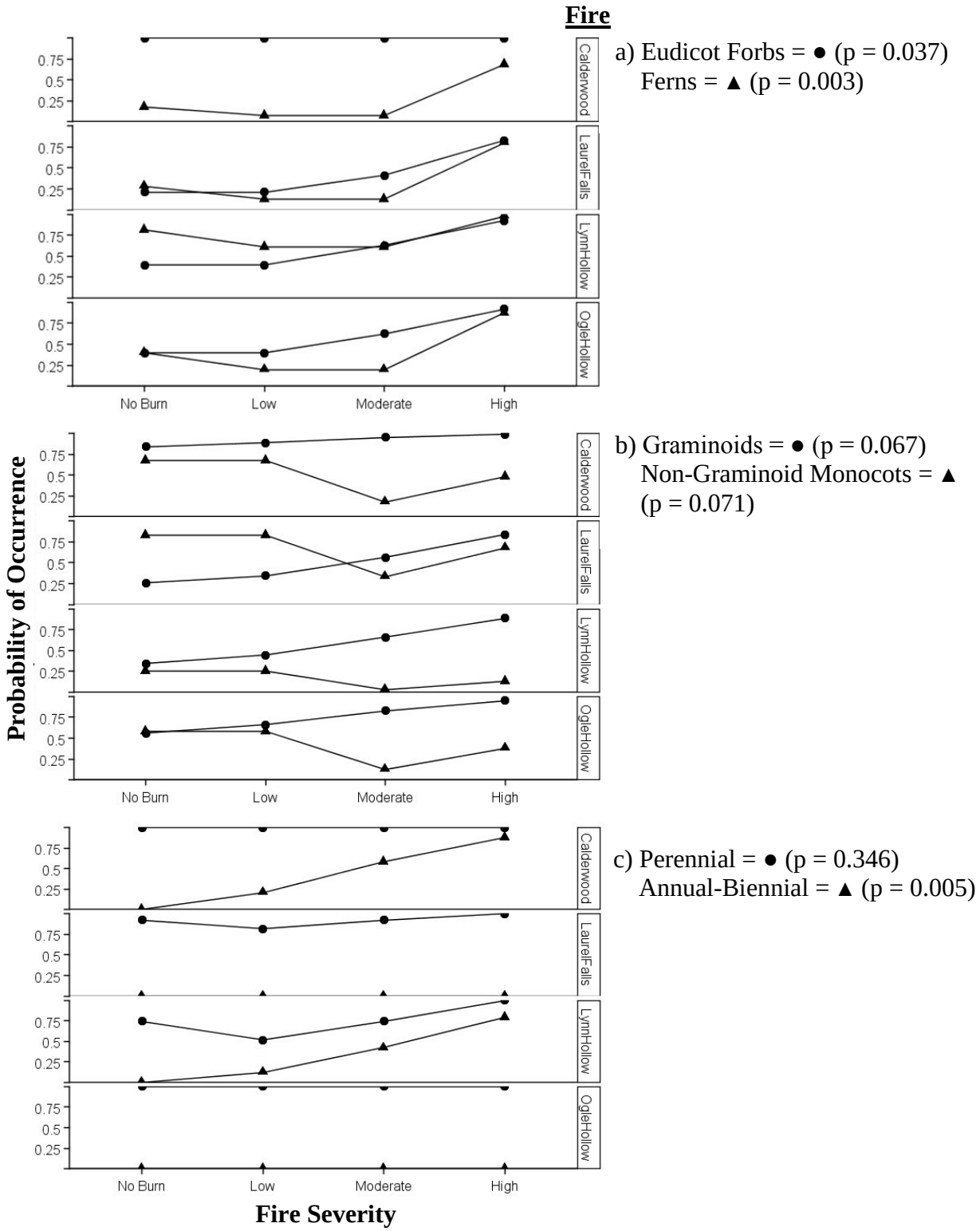
Response Variable	Explanatory Variable	Slope	p-value	R^2
Herb Cover				
	Litter-Duff Depth	-1.70	< 0.001	0.412
	Non-herb Cover	0	0.962	0.002
	Canopy Openness	0.17	< 0.001	0.366
	Subshrub Cover	-0.23	0.0994	0.058
Herb Richness				
	Litter-Duff Depth	-1.18	< 0.001	0.392
	Non-herb Cover	-0.09	0.038	0.090
	Canopy Openness	0.05	0.117	0.053
	Subshrub Cover	-0.36	0.002	0.185
Herb Diversity				
	Litter-Duff Depth	-0.12	0.001	0.211
	Non-herb Cover	-0.02	0.006	0.151
	Canopy Openness	0	0.848	< 0.001
	Subshrub Cover	-0.06	0.005	0.161

Table 6: Multiple regression results for each response variable that included all four explanatory variables with their partial R^2 values and the overall R^2 value for the model. Asterisks indicate significant partial R^2 values. Herb diversity represents the Shannon Diversity Index.

Response Variable	Model	Litter-Duff Depth R^2	Canopy Openness R^2	Subshrub Cover R^2	Non-herb Cover R^2	Overall p-value	Overall R^2
Herb Cover	Log(HerbCover) = 0.007Openness – 0.573log(Duff) – 0.205log(Subshrub) + 0.117log(Non-herb) + 0.882	0.232*	0.136*	0.058*	0.011	< 0.001	0.596
Herb Richness	HerbRichness = 0.007Openness – 9.114log(Duff) – 3.629log(Subshrub) – 0.012Non-herb + 26.375	0.326*	< 0.001	0.103*	0.002	< 0.001	0.559
Herb Diversity	HerbDiversity = -0.0007Openness – 0.739log(Duff) – 0.505log(Subshrub) – 0.431log(Non-herb) + 4.393	0.103*	< 0.001	0.094*	0.038	< 0.001	0.373

MRPP analyses indicated significant differences in herb functional group composition among fire severity classes ($p = 0.030$), although only functional group composition in no burn and high severity areas differed significantly from each other ($p = 0.008$) (Table 4). Eudicot forb cover (1.03%) was slightly more than one-third of the overall herb cover and included 39 species (Table 3). This group included many species in the Asteraceae family, such as five *Solidago* spp., three *Eupatorium* spp., and two *Symphyotrichum* spp. (Table 3). Species of the Fabaceae family were also represented, such as four *Lespedeza* spp. and *Desmodium nudiflorum* (L.) DC. *Lysimachia quadrifolia* L. (Primulaceae) was abundant compared to other species (0.3% cover overall) and *Viola hastata* Michx. (Violaceae) occurred occasionally (6 transects). Logistic regression showed eudicot forb probability of occurrence increased from no burn to high severity, except in the Calderwood fire where eudicot forbs were present in all transects ($p = 0.037$) (Figure 5). Indicator species analysis (ISA) also supported eudicot forbs as an indicator group for high severity areas (indicator value 56.2 out of 100) ($p = 0.013$) (Table 7). Ferns were represented by five species and 0.56% average cover. *Pteridium aquilinum* was the most abundant with 0.54% average cover (Table 3), and was an indicator of high severity areas (Table 7). *Dennstaedtia punctilobula* (Michx.) T. Moore, *Polystichum acrostichoides*, *Asplenium montanum* Willd., and *A. platyneuron* (L.) Britton, Sterns & Poggenb. were the remaining four species (Table 3). Fern probability of occurrence ($p = 0.003$) was highest in high severity areas and slightly higher in no burn compared to low and moderate severity areas (Figure 5). Ferns also had the second-highest indicator value for high severity areas ($p = 0.001$) (Table 7).

Although graminoid species richness (12) was less than one-third of eudicot forb species richness, graminoids had greater average cover (1.18% versus 1.03%, respectively). The *Schizachyrium scoparium*/*Andropogon virginicus* grouping had the greatest average cover



a) Eudicot Forbs = ● (p = 0.037)
Ferns = ▲ (p = 0.003)

b) Graminoids = ● (p = 0.067)
Non-Graminoid Monocots = ▲ (p = 0.071)

c) Perennial = ● (p = 0.346)
Annual-Biennial = ▲ (p = 0.005)

Figure 5: Probability of functional group (a and b) and life cycle group (c) occurrence in each fire.

Table 7: Indicator Species Analysis for functional and life cycle groups, with selected herb species that exhibited statistically significant indicator values. All other herbs and subshrubs were not statistically significant indicators of a particular fire severity class.

Species Group	Indicator Value	Indicated Severity Class	p-value
Functional Groups			
Eudicot Forbs	56.2	High	0.013
Ferns	69.6	High	0.001
Graminoids	80.0	High	0.002
Non-Graminoid Monocots	32.5	No Burn	0.320
Life Cycle Groups			
Perennial	74.4	High	0.002
Annual-Biennial	20.7	High	0.219
Herb Species			
Dichanthelium commutatum	44.6	High	0.020
Pteridium aquilinum	42.2	High	0.046
Schizachyrium scoparium/ Andropogon virginicus	62.0	High	0.004
Scleria sp.	51.3	High	0.001

(1.04%) of the functional group, and *Dichanthelium commutatum* (Schult.) Gould and *Scleria* sp. were also common (Table 3). These species were indicators of high severity areas (Table 7). Among herbs and subshrubs, *D. commutatum* occurred in the most transects (26 out of 48). *Microstegium vimineum* (Trin.) A. Camus was the only invasive herbaceous species recorded during the study with 0.003% average cover, and was found in only one moderate severity transect (Table 3). Probability of graminoid occurrence tended to increase from no burn to high severity ($p = 0.067$) (Figure 5). ISA showed graminoids had the highest indicator value for high severity areas ($p = 0.002$) (Table 7).

Non-graminoid monocots (10 species) had the lowest average cover (0.08%) of the functional groups. Species that occurred most were *Uvularia puberula* Michx., *Maianthemum racemosum*, *Lilium michauxii*, *Cleistes bifaria*, and *Iris verna* L. (Table 3). Non-graminoid monocot occurrence tended to have the highest occurrence in no burn and low severity areas, the lowest occurrence in moderate severity areas, and had an intermediate occurrence in high severity areas ($p = 0.071$) (Figure 5). The non-graminoid monocot indicator value (32.5, highest for no burn areas) was not significant ($p = 0.320$) (Table 7).

Probability of occurrence of annual plus biennial herbs [*Amphicarpaea bracteata* (L.) Fernald, *Erechtites hieraciifolius* (L.) Raf. ex DC., *M. vimineum*, *Polygala polygama* Walter, and *Pseudognaphalium obtusifolium* (L.) Hilliard & B.L. Burtt.] increased with increasing severity ($p = 0.005$) at Calderwood and Lynn Hollow but this group was not present at Ogle Hollow or Laurel Falls (Figure 5). This life cycle group had 0.013% average cover. Most herbs (81%) recorded in this study were confirmed perennial species. There was no significant relationship between probability of perennial herb occurrence and fire severity ($p = 0.346$) (Figure 5). MRPP showed fire severities differed in life cycle group composition ($p = 0.026$, $A = 0.054$), with

pairwise comparisons revealing high severity areas differed from no burn areas ($p = 0.008$) (Table 4). ISA for the two groups showed that both indicator values were highest for high severity areas, but this was significant for perennials ($p = 0.002$) and not for annuals plus biennials (Table 7).

Subshrub cover ranged from 0 to 18.25% and averaged 3.00%. It did not differ among fire severities ($p = 0.866$), but it was weakly and positively related to non-herb cover ($p = 0.036$, $R^2 = 0.092$). Subshrub cover was not related to litter-duff depth ($p = 0.441$) or canopy openness ($p = 0.493$), nor was variation in subshrub cover explained by canopy openness, litter-duff depth, and non-herb cover combined ($p = 0.205$). While only nine species of subshrubs were identified in this study (Table 3), subshrub cover was higher than herbaceous cover (3.00% versus 2.86%, respectively). *Galax urceolata* (1.51%) accounted for half of the total average subshrub cover, and *Gaultheria procumbens* L. (1.28%) made up most of the remaining cover, followed by *Epigaea repens* L. (0.13% average cover). Trends based on averages and occurrences suggest that the subshrubs *Tephrosia virginiana* and *Hypericum hypericoides* occurred more in moderate or high severity areas, while *Chimaphila maculata* declined in abundance from no burn to high severity areas.

When comparing fires, litter-duff depth and non-herb cover was lower at Calderwood (2010) compared to Ogle Hollow (2008), Laurel Falls (2009), and Lynn Hollow (2014) ($p < 0.001$ for each), while canopy openness did not differ ($p = 0.453$) (Table 8). Litter-duff depth was not positively related to time since fire, but canopy openness tended to have a negative relationship with time since fire (Table 8). Herb cover ($p = 0.004$), richness ($p < 0.001$), and Shannon diversity ($p < 0.001$) were higher at Calderwood compared to the other fires, except no difference in herb cover occurred between the Ogle Hollow and Calderwood fires (Table 8).

Table 8: Variation in herbs, subshrubs, non-herb cover, litter-duff depth, and canopy openness among fires (mean ± SE) in GRSM. No burn areas were not included. Different letters indicate significant Tukey test pairwise comparison differences across fires. Herb diversity represents the Shannon Diversity Index.

Variable	Overall Mean	Lynn Hollow	Laurel Falls	Ogle Hollow	Calderwood	p-value
Herb Cover (%)	3.67	0.57 ± 0.22 a	1.27 ± 0.59 a	3.81 ± 3.08 ab	9.04 ± 3.15 b	0.004
Herb + Subshrub Cover (%)	6.88	9.31 ± 1.92	4.83 ± 2.01	4.05 ± 3.06	9.31 ± 3.18	0.273
Herb Richness (#)	6.2	2.3 ± 0.7 a	3.9 ± 0.8 a	4.7 ± 1.1 a	14.0 ± 1.6 b	<0.001
Herb Diversity	0.98	0.37 ± 0.18 a	0.73 ± 0.16 a	0.98 ± 0.24 a	1.83 ± 0.16 b	<0.001
Subshrub Cover (%)	3.20	8.74 ± 2.00 a	3.56 ± 1.65 b	0.24 ± 0.17 b	0.27 ± 0.14 b	<0.001
Non-herb Cover (%)	61.14	59.35 ± 2.45 a	74.49 ± 3.74 b	70.71 ± 4.43 ab	40.01 ± 5.04 c	<0.001
Litter-Duff Depth (cm)	8.1	9.2 ± 0.4 a	8.5 ± 0.8 a	9.8 ± 0.5 a	5.0 ± 0.5 b	<0.001
Canopy Openness (%)	40.55	45.12 ± 0.06	37.77 ± 0.08	37.77 ± 0.06	41.55 ± 0.11	0.453

Herb plus subshrub cover did not differ among the fires (Table 8). Subshrub cover was higher at Lynn Hollow than at the other three fires ($p < 0.001$) (Table 8).

Discussion

The decreasing number of herbaceous species as the number of transects increased (Figure 4) indicates the majority of herb species occurring in the sampled xeric pine-oak forests were recorded during this study. Most herb species (73%) noted by Whittaker (1956) were found in this study, indicating that the historically occurring herbaceous species of xeric pine-oak forests have not disappeared during fire suppression. However, the jackknife estimates of true species richness indicate that many herb species were not recorded because most species identified were uncommon. For example, the uncommon *Baptista tinctoria* (L.) R. Br. and *Sericocarpus asteroides* (L.) Britton, Sterns & Poggenb. were previously reported in xeric pine-oak forests of GRSM (Harrod et al. 2000; Whittaker 1956) but were not identified in this study.

My findings indicate that conditions suitable for herbaceous species, particularly eudicot forbs, graminoids, and ferns, appear to be created by high severity fire but not by low or moderate severity fire, where herb cover responses were similar to no burn areas (Tables 2, 4, and 7, and Figure 5). Other studies have also shown that herbs thrive after high severity fire (Harrod et al. 2000; Huisinga et al. 2005; Jenkins et al. 2011). The relationship between high fire severity and higher herb cover and richness (Table 2) was also illustrated at Calderwood, which occurred late in the growing season during a severe drought (high KBDI) and consisted mostly of high severity areas. Only four of the 48 total strip transects had greater than 19% cover, and three of them were the high severity transects at Calderwood (19.6-21.5%). In xeric pine-oak forests, 20% is typically the upper range for herb cover (Whittaker 1956). It appears that the combination of high severity, late growing season fire, and high KBDI yielded the most

consistently high herb cover, as was also observed by Jenkins et al. (2011).

However, how high severity fire is related to herb cover and diversity can change with time since fire. Pourreza et al. (2014) reported greater herb abundance and diversity in low and moderate severity areas compared to high severity areas one year after a fire. High severity areas have a low viable seed bank (Maia et al. 2012) and low herb cover one year after fire (Harrod et al. 2000) (Table 8, data collection at Lynn Hollow occurred one year after fire) compared to unburned areas, likely because of intense soil heating that reduces seedling growth (Gagnon et al. 2015). Replenishing the seed bank along with colonizer establishment may take more than one year after fire to yield a high abundance of herbs. Higher light availability and more space in high severity areas likely allow herbaceous colonizers to quickly replenish the seed bank and surpass herb cover in low and moderate severity areas in the following years. Herb cover increased between one and three years after fire and was positively related to fire severity (Harrod et al. 2000).

It appears that high severity fire is needed to maintain dominant and less common herbaceous species in xeric pine-oak forests. The two dominant herbs (*Schizachyrium scoparium* and *Pteridium aquilinum*) described by Whittaker (1956) were dominant among herbs and subshrubs only in high severity areas of this study (Tables 2 and 7). Subshrubs were dominant in no burn, low, and moderate severity areas (Table 3), and herbs were not indicators of no burn, low, or moderate severity areas (Table 7). *Pteridium aquilinum* (Arthur et al. 1998; Harrod et al. 2000), *Schizachyrium scoparium*, *Dichanthelium* spp., *Eurybia surculosa*, *Solidago odora*, *Lespedeza hirta* (L.) Hornem., *L. repens* (L.) W.P.C. Barton (Harrod et al. 2000), and *Lysimachia quadrifolia* (Arthur et al. 1998) were also recorded in burned sites of other studies in xeric pine-oak forests and were on average most abundant in high severity areas (Table 3).

Higher abundance of these species helps them persist in xeric pine-oak forests and potentially disperse more broadly throughout these forests.

Griffis et al. (2001) reported substantially higher invasive forb abundance and species richness in high severity compared to unburned areas, while other studies found low invasive herb cover (Huisinga et al. 2005; Jenkins et al. 2011). The only invasive herb (*Microstegium vimineum*) encountered in my study was found in one transect in a moderate severity area in Calderwood, with 0.003% cover overall. The lack of invasive species in the sampled areas is likely due to little human disturbance (Huisinga et al. 2005) prior to the Ogle Hollow, Lynn Hollow, and Laurel Falls fires (GRSM Fire Effects Monitoring Program). When the area of the Calderwood fire was acquired by GRSM about 15 years ago (Rob Klein, GRSM Fire Ecologist, personal communication), it exhibited a high abundance of invasive species but has since been treated mainly for woody invasive species with herbicides (Kristine Johnson, GRSM Supervisory Forester, personal communication). *M. vimineum* is not actively controlled by GRSM.

Non-graminoid monocots were not related to a particular fire severity (Table 7). This is likely because species in the group responded differently across fire severities as a result of species-specific tolerances to fire and disturbance. For example, *Goodyera pubescens* (Willd.) R. Br. (Reddoch and Reddoch 2013), *Iris verna*, and *Chamaelirium luteum* (Funderburk and Skeen 1976) are found in generally undisturbed areas, and this was typically the case in my study (Table 3). Other species such as *Polygonatum biflorum*, *Maianthemum racemosum*, and *Hypoxis hirsuta* were located in low severity or no burn strip transects (Table 3) and have been shown to tolerate fire but not extreme disturbance (Duncan et al. 2008; Holzmueller et al. 2009). *Uvularia puberula* occurred in all severities in my study (Table 3) and appears to be tolerant of fire (Harrod et al. 2000). *Cleistes bifaria* (Gregg 1989) and *Platanthera ciliaris* (Sharp 2004) have

been generally found to be positively affected by fire, and *Lilium michauxii* occurs in fire-adapted communities (Brockway et al. 2006), which explains these species' presence in moderate or high severity areas in my study (Table 3).

Conditions changed by fire severity that likely influence herb species include litter and duff depth and canopy openness. Herb species cover, richness and diversity among fire severity classes were explained primarily by litter-duff depth, along with subshrub cover, but herb cover was also substantially explained by canopy openness. Higher severity fires reduce litter and duff depth (Cocke et al. 2005; Groeschl 1991; Huisinga et al. 2005; Jenkins et al. 2011; as reviewed in Knoepp et al. 2005) (Tables 1, 2, and 8), which is related to higher herb cover and diversity (Jenkins et al. 2011; Sydes and Grime 1981) (Table 5) because a thick duff layer can prevent seeds from germinating (Vazquez-Yanes et al. 1990). Canopy openness increases after higher fire severity due to canopy mortality (Brown et al. 2014; Cocke et al. 2005; Groeschl et al. 1992; Huisinga et al. 2005; Scharenbroch et al. 2012; Welch et al. 2000) (Table 2), and thus more light is available to herbaceous plants. A positive relationship between canopy openness and herb cover was found in my study (Table 5) and other reports (Cipollini et al. 2012; Harrod et al. 2000; Jenkins et al. 2011; Sabo et al. 2009; Small and McCarthy 2002). Increasing canopy openness by harvesting without reducing litter-duff depth has been shown to increase herb species richness compared to undisturbed areas (Small and McCarthy 2002). Despite similar litter-duff depths in moderate and high severity areas (Table 2) and Whittaker's (1956) report of 30% canopy openness for xeric pine-oak forests, which corresponds most closely to what I found in moderate severity areas (33%) (Table 2), herb species cover, richness, and diversity of moderate severity areas were not statistically different from no burn and low severity areas. This may suggest that many herbs that inhabited the open, duff-reduced high severity areas were

colonizers entering after the fire, and there were few seeds in the seed bank or seed viability in the seed bank decreased due to soil heating (Gagnon et al. 2015). The lower canopy openness of moderate severity areas may not have allowed as many herbaceous colonizers to disperse into these areas and establish.

Non-herb cover primarily included trees, shrubs, woody vines, and dead wood, and it was not an important factor in determining herb cover and diversity. Other studies suggest that understory woody density is negatively related to herb cover (Jenkins et al. 2011; Schwartz et al. 2016), with resprouting species after low severity (Arthur et al. 1998; Matlack et al. 1993; Welch et al. 2000) or dormant season (Petersen and Drewa 2009; 2014) fire also leading to reduced light availability and space for herbs. The late growing season fire with high KBDI (Calderwood) had the lowest non-herb cover (Table 8), which indicates high fuel consumption observed in high severity areas (Brown et al. 2014), but herb cover and non-herb cover were not related (Table 5). Non-herb cover was weakly and negatively related to herb species richness and diversity (Table 5), but it did not explain a statistically significant amount of variation in herb cover, richness, or diversity when regressed along with litter-duff depth, canopy openness, and subshrub cover (Table 6). High severity fire that opens the canopy also increases light availability to understory woody species. However, fire that prevents woody species from resprouting, such as high severity (Moreno and Oechel 1991), growing season fire (Drewa et al. 2002) that kills the apical meristem and suppressed buds (Matlack et al. 1993; Welch et al. 2000) and underground organs of hardwood species (Johnson 1996) like what may have occurred at Calderwood appears to allow herbs to thrive (Table 8).

The most common subshrubs in xeric pine-oak forests described by Whittaker (1956) matched the most common subshrubs in this study (*Galax urceolata*, *Gaultheria procumbens*, and *Epigaea repens*). Subshrub cover was not related to fire severity (Table 2), litter-duff depth,

or canopy openness in my study; however, Whittaker (1956) noted that the common subshrubs are particularly abundant under dense heath shrubs. Subshrub cover was weakly but positively related to non-herb cover. While not statistically significant, subshrubs tended to occur more abundantly in fires (Lynn Hollow and Laurel Falls) with high *Kalmia latifolia* and low yellow pine understory cover, and among non-herbs, the most common subshrubs were most associated with *K. latifolia*. This suggests that similar environmental conditions, which could be independent of fire, might be required by *K. latifolia* and subshrubs to thrive or that *K. latifolia* might help create the environmental conditions required by subshrubs.

Furthermore, subshrubs appear to be occurring in place of herbs where herb cover is low, and herb and subshrub groups are maintaining a similar amount of cover across xeric pine-oak forests. When comparing only herb cover among the four fires sampled including no burn areas, it is highest at the late growing season fire compared to the rest of the fires. However, herb plus subshrub cover did not differ among the fires (Table 8). In addition, subshrub cover was negatively related to herb richness and diversity (Table 8). Since subshrubs were dominant except in high severity areas (Table 3), it appears that subshrubs were allowed to dominate over herbs in xeric pine-oak forests during fire suppression when disturbances were less frequent. Because of the differing responses to fire by herbs and subshrubs, these groups should not be aggregated into one category as previous studies have done (Whittaker 1956). Additionally, subshrubs should be recorded as a separate category instead of including them with understory woody species (Arthur et al. 1998; Harrod et al. 2000) to better examine their relationship with herbs.

Management Implications

High severity fire is needed to reduce litter-duff depth, increase canopy openness, and

increase herb species cover and richness, especially of eudicot forbs, ferns, and graminoids. However, fire-intolerant non-graminoid monocots may be lost when using this strategy, but fire-tolerant species, such as *Platanthera ciliaris* and *Cleistes bifaria*, will likely thrive. Fires occurring late in the growing season or during droughts may be the most effective at reducing fuel load and increasing herb cover, richness, and diversity of herbs due to their higher severity. However, these fires are more difficult to control. It is possible that if the pre-fire suppression fire interval of 12.7 years is restored to xeric-pine forests (Harmon 1982) and successfully creates conditions appropriate for xeric pine-oak understories, high severity fire might not be needed to maintain the herbaceous communities. More research is needed that combines fire severity and frequency. Studies are also needed to better understand the relationship between herbs and subshrubs, which occupy the same forest layer. More research is needed on how herb communities and subshrubs respond to fire season and drought during a fire. While this study provides some understanding of this, it was not designed to examine differences among fire seasons and drought.

CHAPTER 4: LITERATURE CITED

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Appendix A: Supplemental Tables and Figures

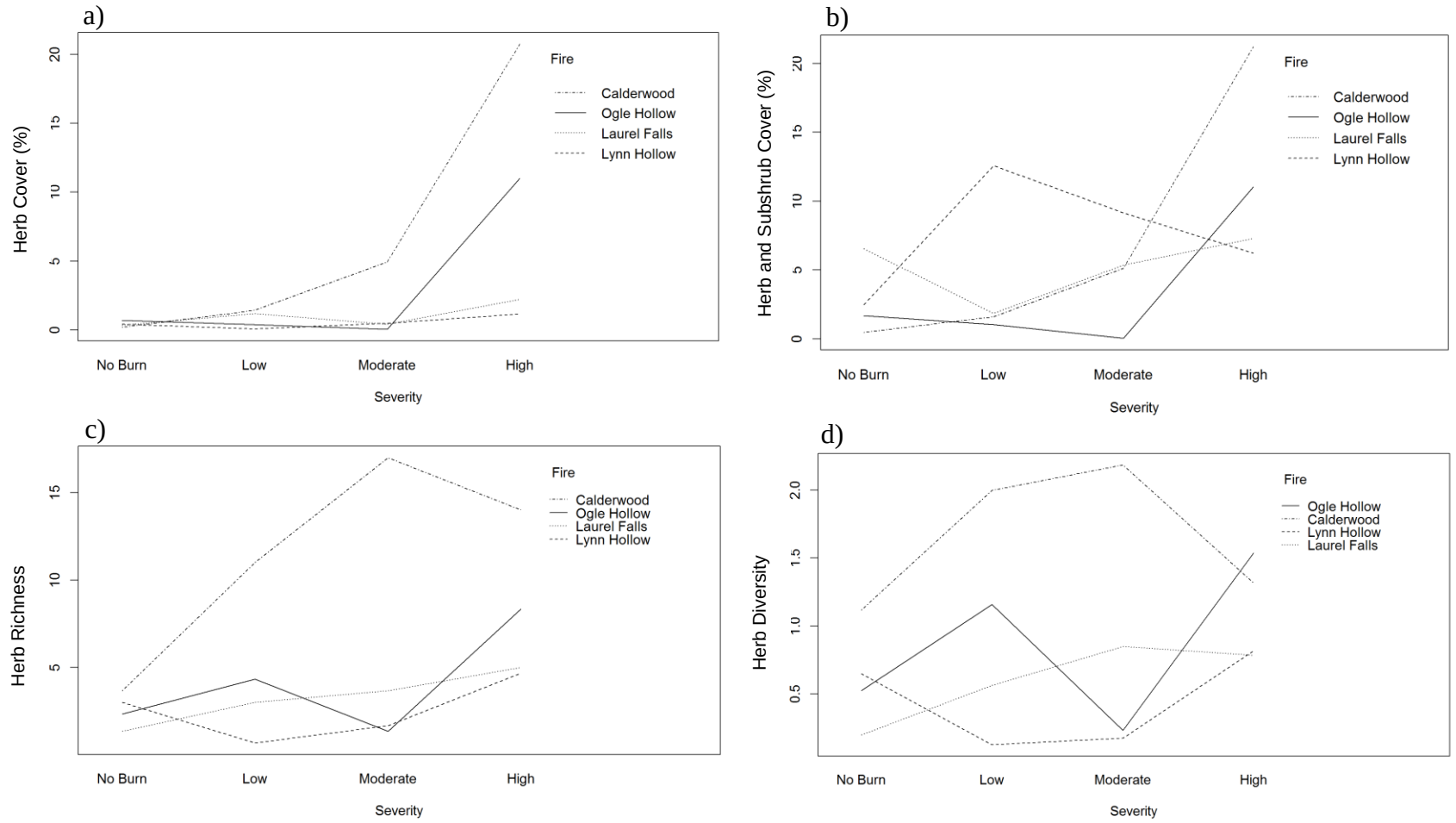

Figure A1: Response of (a) herbaceous cover, (b) herb plus subshrub cover, (c) herbaceous species richness, and (d) Shannon Diversity Index of herbs across fire severity classes for each fire.

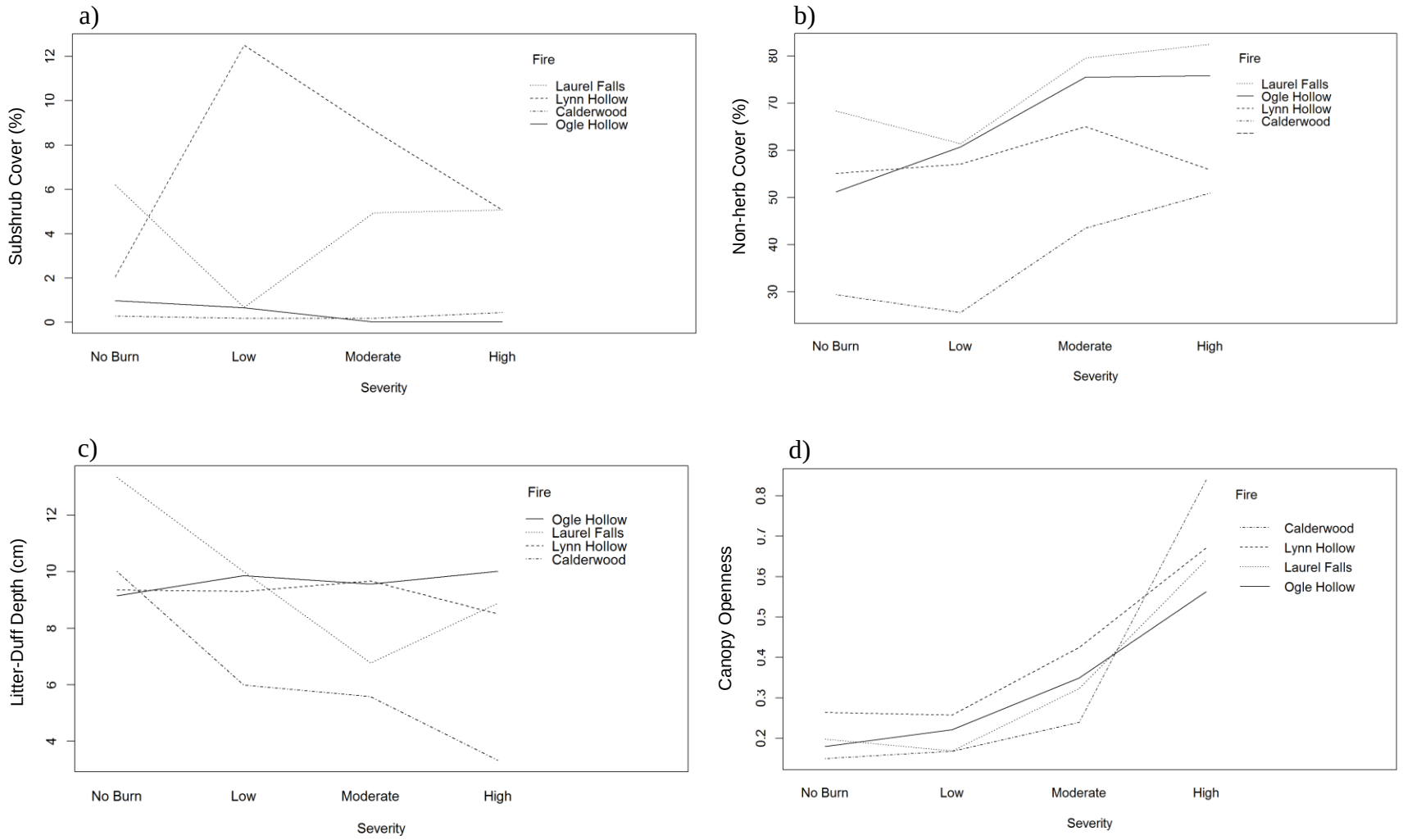

Figure A2: Response of (a) subshrub cover, (b) non-herb cover, (c) litter-duff depth, and (d) canopy openness across fire severity classes for each fire.

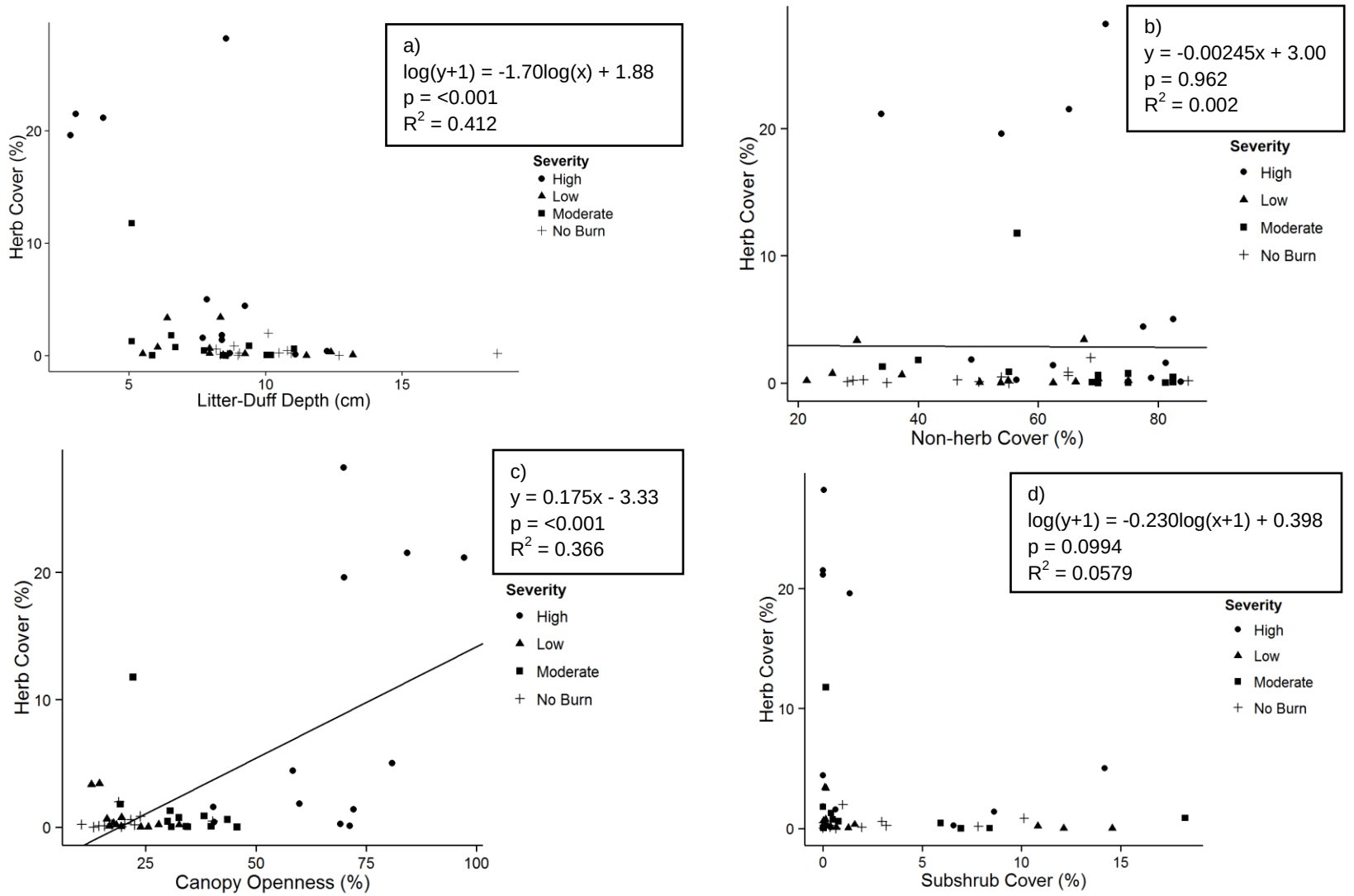

Figure A3: Relationships between herbaceous cover and (a) litter-duff depth, (b) non-herb cover, (c) canopy openness, and (d) subshrub cover. The original data are graphically represented. Each data point represents average values in one strip transect.

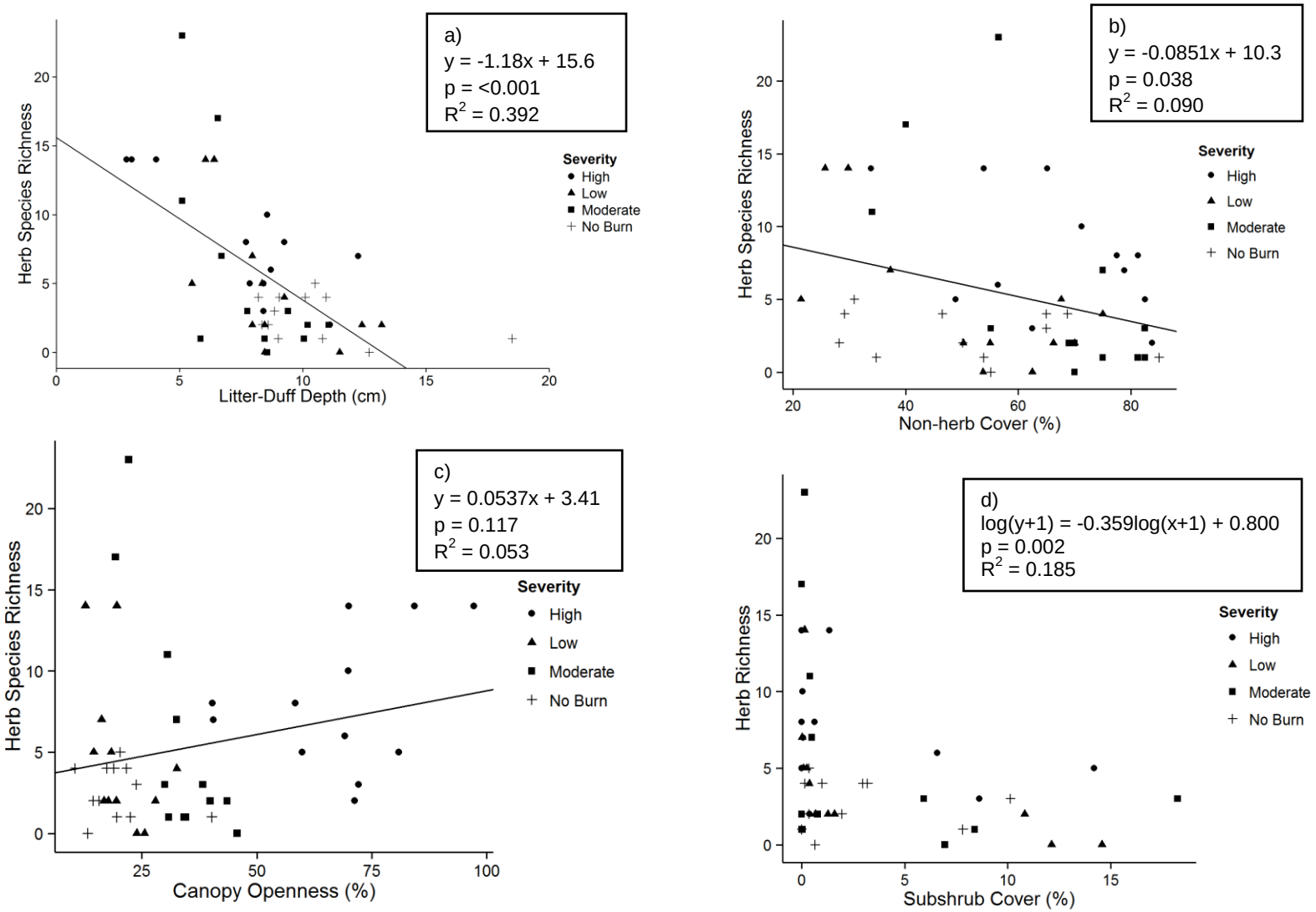

Figure A4: Relationships between herbaceous species richness and (a) litter-duff depth, (b) non-herb cover, (c) canopy openness, and (d) subshrub cover. The original data are graphically represented. Each data point represents average values in one strip transect.

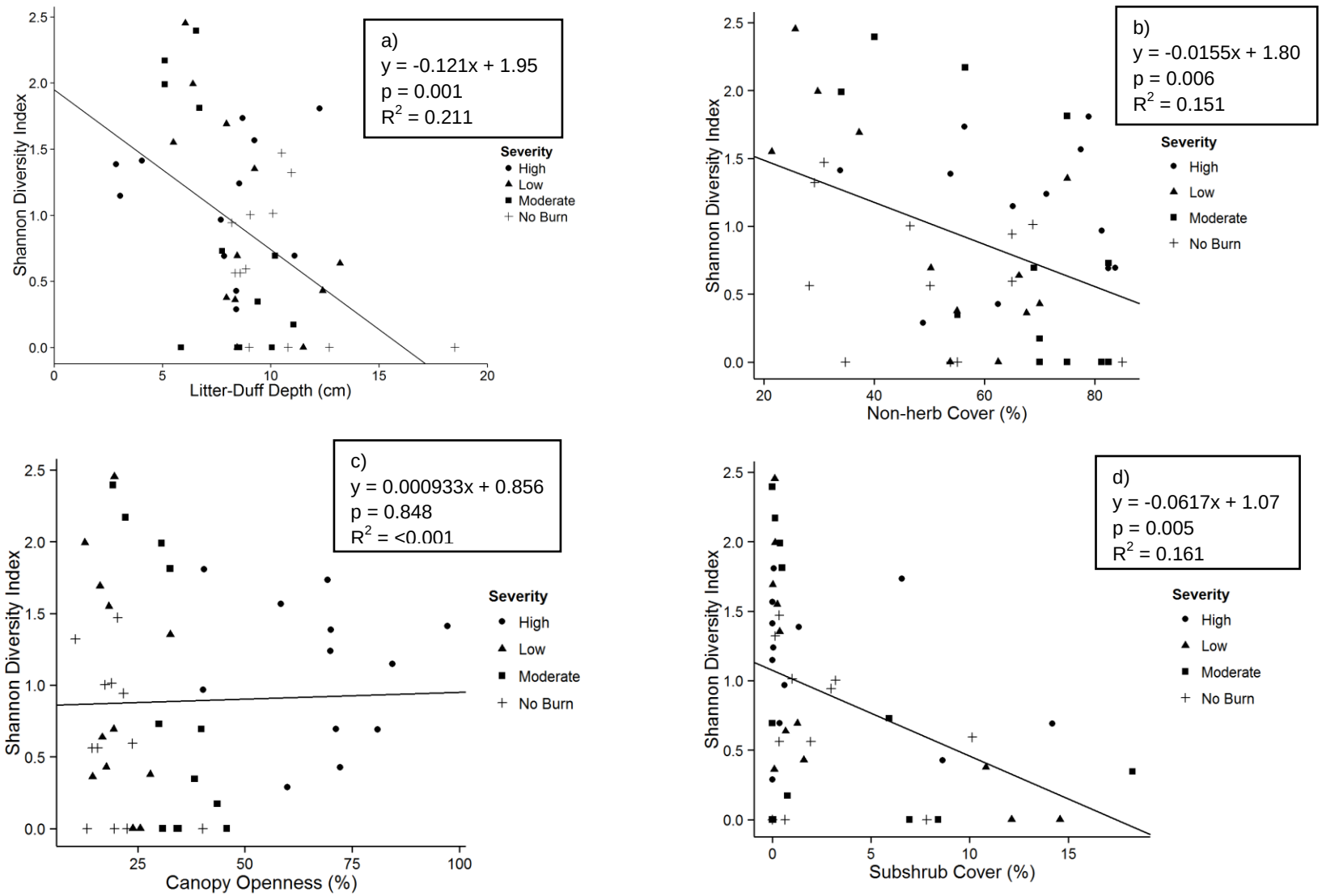

Figure A5: Relationships between the Shannon Diversity Index of herbs and (a) litter-duff depth, (b) non-herb cover, (c) canopy openness, and (d) subshrub cover. The original data are graphically represented. Each data point represents average values in one strip transect.

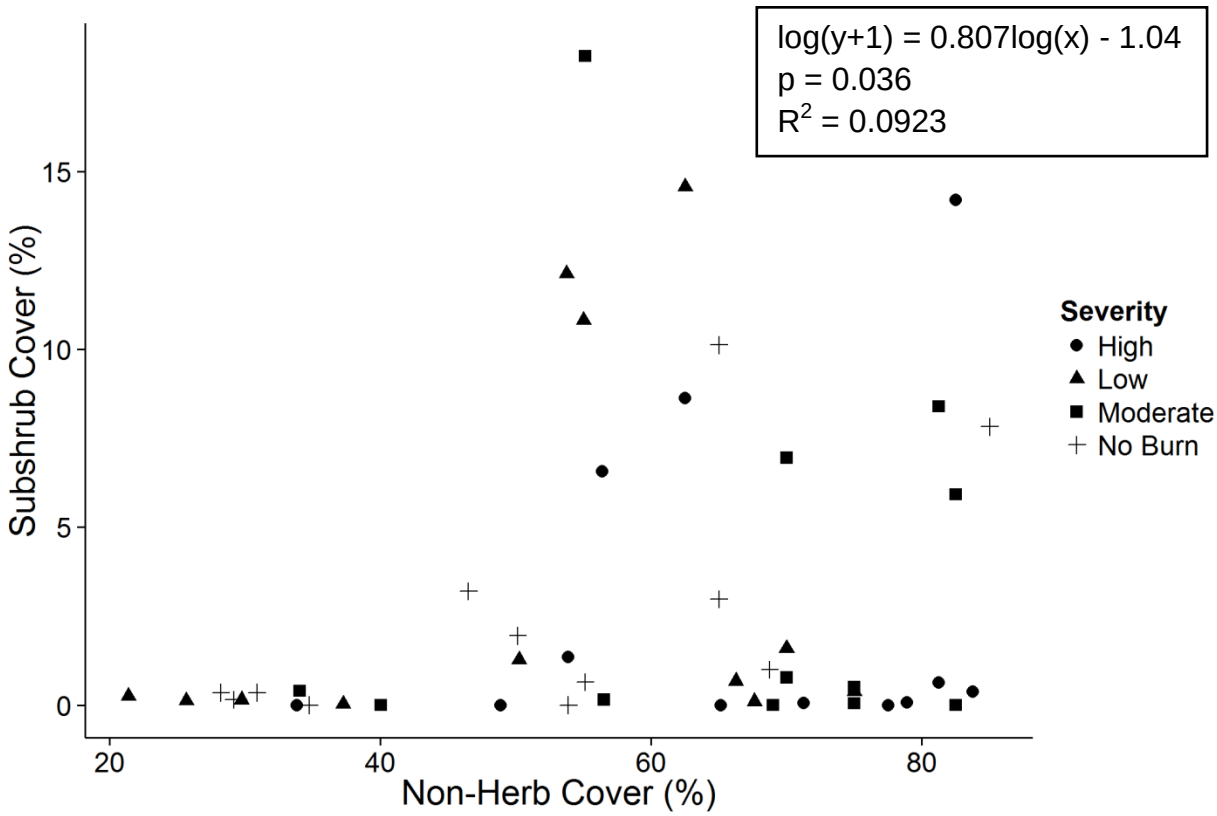

Figure A6: Relationship between subshrub cover and non-herb cover. The original data are graphically represented. Each data point represents the average values in one strip transect.

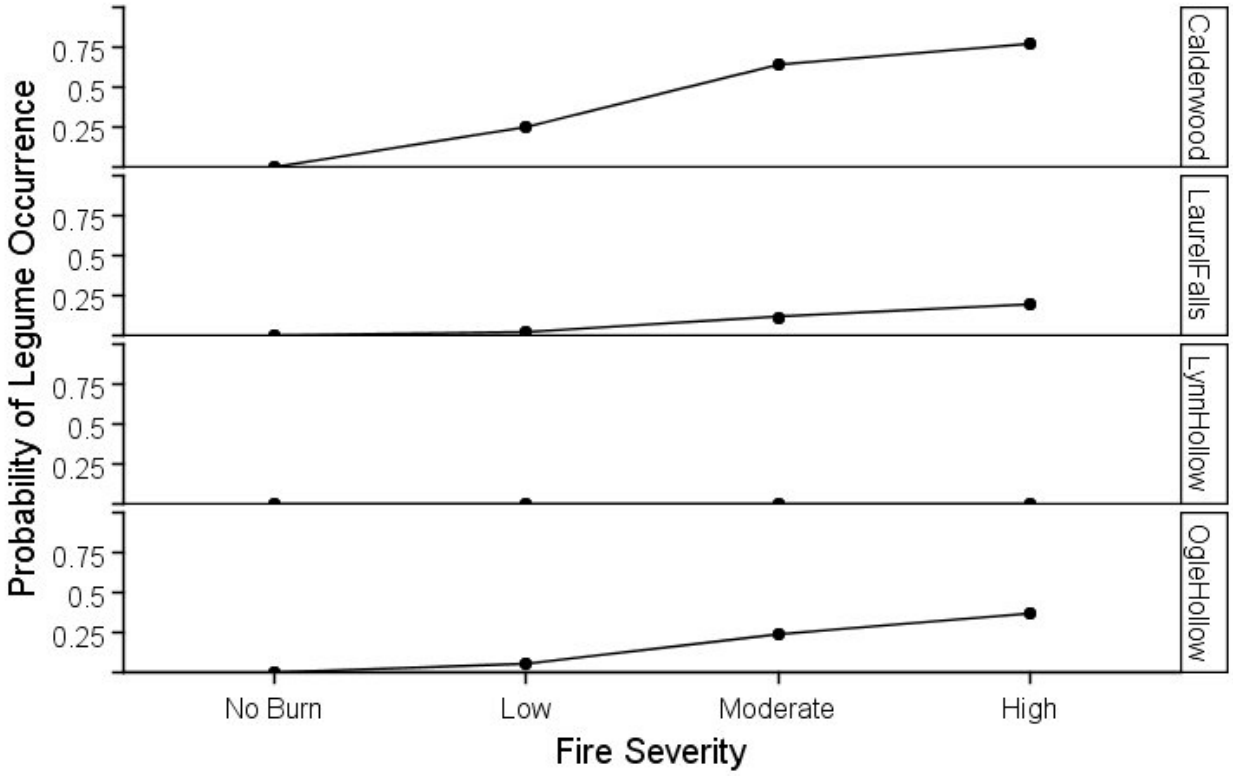

Figure A7: Probability of legume occurrence in each fire sampled in this study. The p-value for differences among fire severity classes is 0.028.

Table A1: Herbaceous and subshrub species recorded grouped by functional group and by family. Nomenclature follows USDA and NRCS (2016).

Eudicot Forbs

Apiaceae
Taenidia integerrima (L.) Drude

Aristolochiaceae
Aristolochia serpentaria L.

Asteraceae
Ageratina altissima (L.) R.M. King & H. Rob.
Antennaria sp.
Coreopsis major Walter
Erechtites hieraciifolius (L.) Raf. ex DC.
Eupatorium rotundifolium L.
E. serotinum Michx.
E. sessilifolium L.
Eurybia surculosa (Michx.) G.L. Nesom
Eutrochium purpureum (L.) E.E. Lamont
Hieracium venosum L.
Lactuca sp.
Pityopsis graminifolia (Michx.) Nutt.
Pseudognaphalium obtusifolium (L.) Hilliard & B.L. Burtt
Silphium asteriscus L.
Solidago arguta Aiton
S. canadensis L.
S. curtisii Torr. & A. Gray
S. odora Aiton
Solidago sp.
Symphyotrichum patens (Aiton) G.L. Nesom
S. undulatum (L.) G.L. Nesom
Asteraceae sp.

Caryophyllaceae
Stellaria sp.

Fabaceae
Amphicarpaea bracteata (L.) Fernald
Lespedeza hirta (L.) Hornem.
L. repens (L.) W.P.C. Barton
L. violacea (L.) Pers.
Lespedeza sp.
Desmodium nudiflorum (L.) DC.

Lamiaceae
Pycnanthemum sp.

Table A1 Continued

Polygalaceae
Polygala polygama Walter

Primulaceae
Lysimachia quadrifolia L.

Rosaceae
Potentilla sp.

Rubiaceae
Houstonia longifolia Gaertn.

Violaceae
Viola hastata Michx.
V. palmata L.
Viola sp.

Ferns

Aspleniaceae
Asplenium montanum Willd.
A. platyneuron (L.) Britton, Sterns & Poggenb.

Dennstaedtiaceae
Dennstaedtia punctilobula (Michx.) T. Moore
Pteridium aquilinum (L.) Kuhn

Dryopteridaceae
Polystichum acrostichoides (Michx.) Schott

Graminoids

Cyperaceae
Carex hirsutella Mack.
Carex sp.
Scleria sp.
Cyperaceae sp.

Poaceae
Dichanthelium boscii (Poir.) Gould & C.A. Clark
D. commutatum (Schult.) Gould
D. dichotomum (L.) Gould
D. villosissimum (Nash) Freckmann
Dichanthelium sp.
Microstegium vimineum (Trin.) A. Camus
Schizachyrium scoparium (Michx.) Nash/
Andropogon virginicus L.
Sorghastrum nutans (L.) Nash

Table A1 Continued

Non-Graminoid Monocots
Iridaceae
Iris verna L.
Liliaceae
Chamaelirium luteum (L.) A. Gray
Hypoxis hirsute (L.) Coville
Lilium michauxii Poir.
Maianthemum racemosum (L.) Link
Polygonatum biflorum (Walter) Elliott
Uvularia puberula Michx.
Orchidaceae
Cleistes bifaria (Fernald) Catling & Gregg
Goodyera pubescens (Willd.) R. Br.
Platanthera ciliaris (L.) Lindl.
Fern Ally
Lycopodiaceae
Dendrolycopodium obscurum (L.) A. Haines
Subshrubs
Diapensiaceae
Galax urceolata (Poir.) Brummit
Ericaceae
Chimaphila maculata (L.) Pursh
Epigaea repens L.
Gaultheria procumbens L.
Fabaceae
Chamaecrista nictitans (L.) Moench
Tephrosia virginiana (L.) Pers.
Hypericaceae
Hypericum hypericoides (L.) Crantz
Rubiaceae
Galium circaezans Michx.
Mitchella repens L.

Appendix B: Spring Data Collection Methods and Results

Methods

Methods followed were identical to those described in Chapter 3 with the exceptions noted below. Within each fire, transects were located in the same soil type according to GRSM's soil taxonomic classification map. I sampled one strip transect per fire severity class for each of the four fires. A "no burn" severity class was not included in the spring data collection. Therefore, with three severity classes and four fires, 12 transects were included in the study. Strip transects were at least 30 m apart or more. Strip transects were divided into forty 1 × 1 m quadrats to measure herb and woody percent cover and litter-duff depth. Total living woody (trees, shrubs, and woody vines) cover that was rooted in the strip transect and up to 1 m above the ground was measured wherever herbaceous plant species occurred. Spring data collection occurred from May 4, 2015 to May 22, 2015.

Results

Table B1: P-values from ANOVAs conducted on the spring data. Severity indicates the fire severity class (Low, Moderate, and High) and Fire indicates the burned area (Calderwood, Laurel Falls, Lynn Hollow, and Ogle Hollow). Herb diversity represents the Shannon Diversity Index.

Source of Variation	Herb Cover	Herb Richness	Herb Diversity	Subshrub Cover
Severity	0.285	0.334	0.622	0.505
Fire	0.473	0.011	0.054	0.510

Table B2: Variation among fire severity classes (mean ± SE) for herbs and subshrubs from the spring data collection. Herb diversity represents the Shannon Diversity Index.

Variable	Overall Mean	Low	Moderate	High	p-value
Herb Cover (%)	2.36	0.45 ± 0.35	0.32 ± 0.27	6.30 ± 4.69	0.285
Herb Richness (#)	4.8	5.0 ± 2.7	3.3 ± 2.0	6.3 ± 2.9	0.334
Herb Diversity	0.71	0.87 ± 0.41	0.51 ± 0.32	0.76 ± 0.42	0.622
Subshrub Cover (%)	1.07	2.39 ± 2.24	0.75 ± 0.57	0.06 ± 0.06	0.505

Table B3: Relationships among herbs and subshrubs during the spring data collection. Herb diversity represents the Shannon Diversity Index.

Response Variable	Explanatory Variable	Linear Regression Equation	p-value	R^2
Herb Cover	Subshrub Cover	$\log(y+1) = -0.440\log(x+1) + 0.795$	0.283	0.114
Herb Richness	Subshrub Cover	$\log(y+1) = -0.650\log(x+1) + 1.68$	0.0829	0.271
Herb Diversity	Subshrub Cover	$\log(y+1) = -0.301\log(x+1) + 0.574$	0.0984	0.249

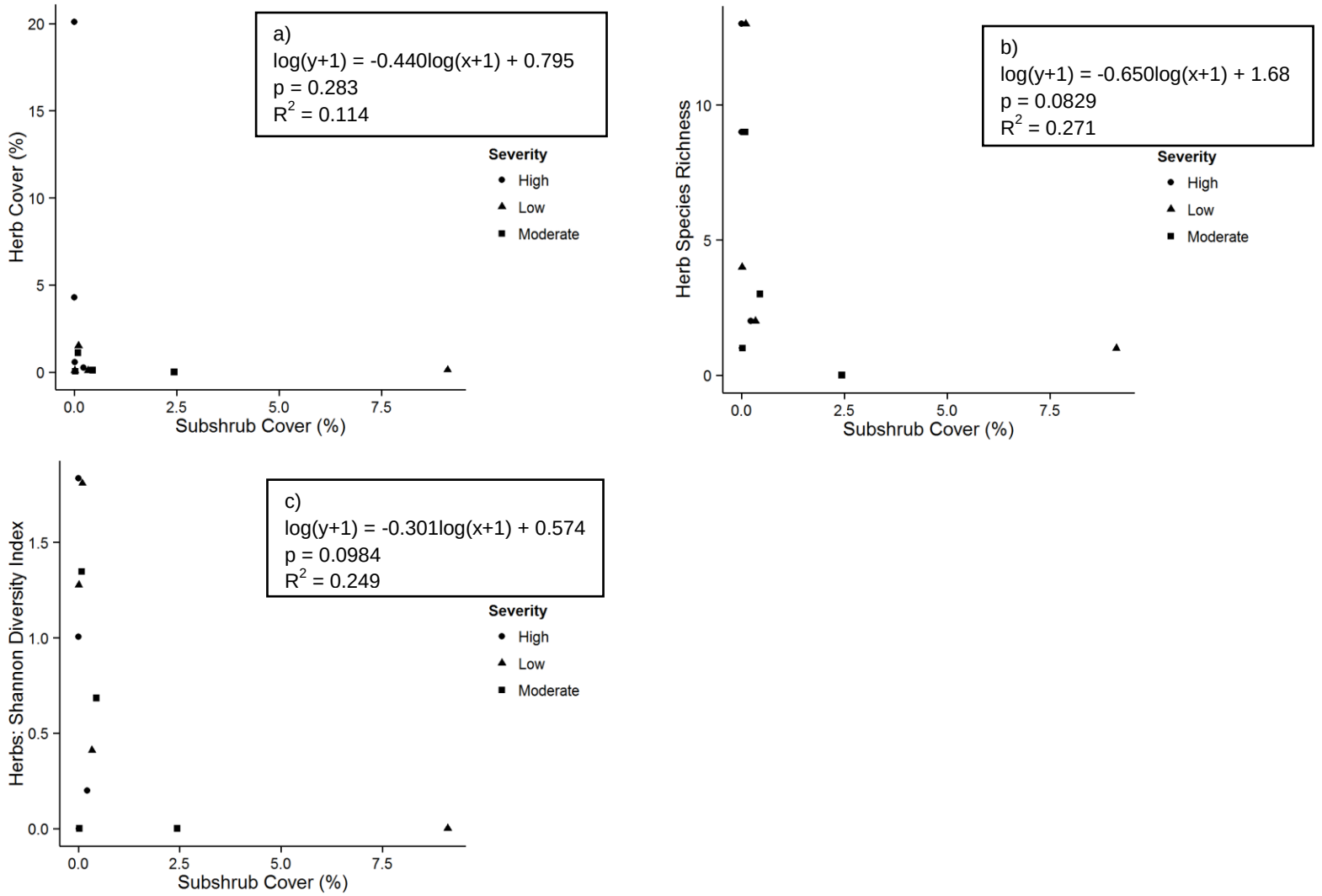

Figure B1: Relationship between subshrub cover and (a) herbaceous cover, (b) herb species richness, and (c) Shannon Diversity Index of herbs. The original data are graphically represented. Each data point represents the average values in one strip transect.

Table B4: Herbaceous and subshrub species percent cover recorded in four fires in GRSM (mean ± SE) during the spring data collection. All SE are <0.01% unless otherwise noted. Count indicates the number of strip transects in which a species occurred.

	Overall	----------Fire Severity----------			
	Mean	Low	Moderate	High	Count
Herbs					
Ageratina altissima	0.04	<0.01	0	0.13±0.13	2
Coreopsis major	<0.01	0.01±0.01	0.01	0	3
Desmodium nudiflorum	0.01	0.02±0.02	0.01±0.01	0	2
Dichanthelium boscii	<0.01	<0.01	0	0	1
Dichanthelium commutatum	0.02	<0.01	0.01±0.01	0.03±0.03	3
Dichanthelium sp.	0.01	0.03±0.03	<0.01	0.02±0.02	3
Eupatorium capillifolium	0.01	0	0	0.02±0.02	1
Eurybia surculosa	0.07	0	<0.01	0.22±0.21	3
Hypoxis hirsuta	<0.01	0.01±0.01	<0.01	0	2
Lactuca sp.	<0.01	0	0	0.01±0.01	1
Lespedeza violacea	0.01	0	0	0.03±0.03	1
Lilium michauxii	<0.01	<0.01	0	<0.01	2
Lysimachia quadrifolia	0.10	0	0.15±0.15	0.16±0.10	3
Maianthemum racemosum	0.01	0.03±0.03	0	0	1
Pityopsis graminifolia	0.04	0	0	0.11±0.11	1
Potentilla sp.	<0.01	<0.01	0	0	1
Pteridium aquilinum	1.11	0.05±0.03	0.04±0.03	3.22±3.03	6
Schizachyrium scoparium	0.50	0	0	1.49±1.49	1
Schizachyrium scoparium/ Andropogon virginicus	0.16	0.14±0.14	<0.01	0.34±0.34	3
Scleria sp.	<0.01	0	0	0.01±0.01	2
Sericocarpus linifolius	<0.01	0	0	0.01±0.01	1
Solidago arguta	0.13	0.11±0.11	0.02±0.02	0.27±0.24	4
Solidago odora	<0.01	0	0	<0.01	1
Sorghastrum nutans	0.02	0	0	0.07±0.07	1
Taenidia integerrima	<0.01	0.01±0.01	0	0	1
Tipularia discolor	<0.01	<0.01	0	0	1
Uvularia puberula	0.01	0.02±0.01	0	0	2
Viola hastata	0.03	0.01±0.01	0.07±0.07	0.01±0.01	4
Asteraceae sp.	0.05	0	0	0.16±0.16	1
Subshrubs					
Chimaphila maculata	0.02	0.03±0.02	0.03±0.02	0	4
Epigaea repens	0.05	0.07±0.04	0.08±0.08	<0.01	4
Galax urceolata	0.68	1.81±1.76	0.16±0.16	0.06±0.06	4
Gaultheria procumbens	0.32	0.48±0.48	0.48±0.44	0	3